

SPIKELET VARIATION IN *ZEA MAYS* L.*

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INTRODUCTION

In classifying the different varieties of Indian corn, *Zea Mays*, scientists have paid little attention to comparative floral morphology. Since the kernel is economically the most important part of the maize plant nearly all classifications have been based on its texture and morphology. The most recent classification is that of Sturtevant (1899), which is based on the characteristics of kernel texture and the development of husks around individual kernels. We may summarize Sturtevant's classification as follows:

Zea tunicata, the pod corns: "each kernel is inclosed in a pod or husks."

Zea everta, the pop corns: "characterized by the excessive proportion of the corneous endosperm and the small size of the kernels and ear."

Zea indurata, the flint corns: "readily recognized by the occurrence of a starchy endosperm inclosed in a corneous endosperm."

Zea indentata, the dent corns: "recognized by the presence of corneous endosperm at the sides of the kernel, the starchy endosperm extending to the summit."

Zea amylacea, the soft corns (the flour corns): "recognized by the absence of corneous endosperm."

Zea saccharata, the sweet corns: "a well-defined species group characterized by the translucent, horny appearance of the kernels and their more or less crinkled, wrinkled, or shriveled condition."

As Anderson and Cutler (1942) have pointed out, this classification is an artificial one and is of aid only in cataloguing different varieties. It does not indicate relationships between different groups or varieties.

Details of floral morphology are among the most important characters in the taxonomy of grasses. Although all the maize varieties, as far as we know, belong to one botanical species, investigations made thus far have shown that comparative morphological studies of reproductive organs can be of great importance. During their long existence many of the varieties of maize have become fairly constant. In some cases the morphological differences between different strains of maize are like those between closely related species of wild grasses.

Not only does the study of the spikelets of the tassel give us a new character for understanding the natural classification of the present-day varieties of maize, but it may also give important clues to the origin of these varieties. During the

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last decades archeological discoveries in several different localities in North and South America have yielded interesting prehistoric and pre-Columbian material. The great majority of these maize remains which have found their way into museums are ears, shelled cobs, and loose kernels. Fewer tassels have been excavated and catalogued but still there is a fair number of tassels and tassel fragments, enough at least to give a clear picture of the characteristics of that part of the plant. The best of these remains are extremely well preserved although hundreds, or even thousands, of years old, and they can accurately be compared with material obtained from present-day varieties. By comparing archeological maize remains with each other, one can determine variation in prehistoric times. By comparing modern varieties with archeological material it is possible to show in which characters and to what extent changes have taken place. Until we have learned to know the ancient varieties, we shall not be able to understand the differences in modern varieties. Knowing now some of the primitive types of maize we are able to tell something more about the migrations of Indian corn from one area to another, perhaps even from one continent to another.

Both male and female flowers and inflorescences deserve study. There are, however, many external and mechanical factors which cause complicated differences in female spikelets, such as the pressure of the husk leaves, the pressure between kernels in the ear, the development of bony tissues, etc. Male spikelets, on the contrary, develop free in the open tassels and are much easier to handle and prepare than female ones, which are always partly hard and bony, partly thin and membranaceous.

For practical corn breeding the knowledge of both tassel and male spikelet characters is a valuable tool. Since the tassels reach maturity early in the growing season, the corn breeder can tell something about the offspring by knowing the male spikelet character, long before the kernels and ear show any of their mature characteristics. The present paper is a beginning at analyzing the variation of the male spikelets of maize. It is an attempt to determine in which characteristics variation takes place and how it can best be measured.

PREVIOUS MORPHOLOGICAL STUDIES

REVIEW OF LITERATURE

The first morphological studies of *Zea Mays* were concentrated almost entirely on the origin and the structure of the female inflorescence. In them students were trying to understand the complicated structure of the ear of maize. So much did this structure intrigue them that virtually no studies of the male inflorescence were made until the twentieth century.

In recent decades, in analyzing the male inflorescence, several workers have noted rather marked morphological correlation between it and the female inflorescence. The type of correlation is usually referred to as the "homology of the ear and tassel." The earliest discussion of this idea is found in a paper by Mrs. W. A.

Kellerman (1895). It was her opinion that primitive maize had been a plant branching from many nodes, each branch with a terminal inflorescence similar to the maize tassel of the present day, but with bisexual flowers. Through selection the male flowers became more numerous in the terminal inflorescence of the main stem, while the female flowers became more numerous in the inflorescences of the lateral branches. Being in a more favorable position as regards nutrition, the central axis of the inflorescences in the lateral branches developed more strongly, while the branches of these inflorescences became reduced; as Kellerman puts it:

The central stem of the "tassel" borne by the primitive branch by virtue of its more favorable position drew into itself the main force of the branch and became more highly developed at the expense of the surrounding tassel branchlets, the latter being finally entirely aborted. (Kellerman, 1895, p. 44).

Kellerman's statement, although not based on any reported detailed studies, made later students of the maize plant pay more attention to the question of the homology of the maize ear and tassel.

In attempting to explain the difference in the structures of the central spike and of the rest of the tassel, Collins came to the conclusion that:

If one assumes a profusely branched panicle in which the branches have been reduced until each branch is represented by a single pair of spikelets, the inflorescence becomes a spike. If such a reduction of branches is confined to the upper part of the inflorescence, a type is produced resembling that of maize. (Collins, 1912, p. 526).

A more detailed study of the structure and phylogeny of the maize tassel was first made by Weatherwax (1935). He studied a number of inflorescences of different species of grasses, both related and unrelated to maize, and came to the conclusion that the present-day maize tassel, a compound inflorescence of a number of raceme-like branches having their spikelets in pairs, may be a result of several steps in evolution. It may have developed from a primitive type of inflorescence, a panicle with loose branches, the spikelets not arranged in pairs. The raceme-like structure of the branches of the maize tassel and the arrangement of the spikelets in pairs may have had an independent evolution since grasses of several genera, not closely related to each other or to maize, have one or the other of these characters in their inflorescences or, as in maize, both.

The development of both the male and female inflorescences of maize was first studied by Bonnett (1940). He discovered that from the germination of the kernel to the dehiscence of the anthers the plant passes through two stages. In the first, only vegetative parts, leaves and axillary shoots, are produced, while the differentiation and development of the inflorescences take place in the second stage. In the tassel the secondary branches develop first, and from their bases the tertiary branches later start their development.

As mentioned previously, the classification of maize varieties made by Sturtevant (1899) was an artificial one. Anderson and Cutler (1942), realizing the need for a more natural classification, studied the external morphological characters of maize which would be useful criteria for the descriptions of strains and varieties.

The number of tassel branches was found to be surprisingly stable for a variety and to be one of the most useful characteristics. The stiffness of the tassel branches, the length of the sterile zone at the base of the secondary branches, the degree of variation in the spikelet and the arrangement of the spikelets, and the presence and degree of condensation were found to be some of the best characters for distinguishing different varieties. By "condensation" is understood the situation in the secondary branches, where the internodes are so telescoped together that several spikelet pairs appear whorled at one node instead of being alternate at several nodes.

Although the homology of the ear and tassel had been suggested by several earlier authors it had not been investigated in detail until the studies of Anderson (1944b). Around 1940 he began to study the morphological correlation between the male and female inflorescences, realizing that a thorough knowledge of the maize tassel is not only important as such but is also the best key for understanding the phenomena of the ear. The characteristics which are so closely correlated with each other in these two inflorescences are much more readily studied in the tassel. While working with many different varieties of maize, Anderson studied the cause of row numbers above 8 and 10 and found row number to be correlated with condensation, a correlation particularly close in North American varieties. After more detailed studies, Anderson and Brown (1948) came to the same conclusion.

Another important fact found by Anderson (1944b) is the close correspondence between the relative and absolute lengths of the secondary tassel branches, on the one hand, and the shape and size of the ear, on the other. The presence of tertiary branches was found to be correlated with the irregular arrangement of the kernels at the base of the ear—a character relatively common in certain varieties of maize.

While condensation is rather common in some North American races of maize it is much less so in South America. There multiplication, a phenomenon which also increases the number of kernels on the ear, is more common than it is in North America. Multiplication has been described by Cutler (1946, p. 269) as producing tassels "with the sessile and pedicellate spikelets alternating at the nodes as if the primordia had branched to give rise to more pairs of spikelets."

Studies on the homology of the ear and tassel of maize, as well as on the morphology of different tassel characters, have given a clearer picture of the phenomena in both of the inflorescences. Bonnett (1948) found that at the early stages the tassel and ear are morphologically scarcely distinguishable from each other. At a certain stage of development the ear becomes progressively thicker and harder and the tassel progressively more lax and expanded. According to Kiesselbach (1949), the differentiation of the ear and tassel begins very early, and three weeks after planting, the entire stem, surmounted by the differentiated tassel, may have been formed.

Just as the earlier students of maize concentrated their attention upon the female inflorescence, the ear, so in studying the spikelet did they devote themselves

almost completely to the pistillate flowers. In Malpighi's 'Anatome Plantarum' of 1675 (Arber, 1934, p. 362) appears what is perhaps the first illustration of the staminate spikelet of maize, an illustration which clearly shows the different parts of the spikelet. Despite this early example of careful attention to the details of the staminate spikelet nearly two and a half centuries elapsed before further progress was made.

Weatherwax, in his study of anomalous flowers in maize (1925), mentions that the primordia of the two spikelets appear at an early stage of development, and that the upper primordium, which later becomes a pedicellate spikelet, is regularly the more advanced. Bonnett (1948) discovered that at the beginning of spikelet formation the branch initials, which already are unequal, divide into two parts. The larger becomes the pedicellate spikelet and the smaller the sessile one. In the staminate spikelet flowering parts differentiate in this order: first, the empty glumes, then the flowering glumes, and finally the anthers, the differentiation and development of the anthers being the main growth activities. The pistil may start to develop, but usually it remains rudimentary. Kiesselbach (1949) found that the flower formed at the original growing point of the spikelet is the terminal one; the lower flower is developed from the growing point which is somewhat later formed at the axil of the lower glume. Cutler and Cutler (1948) have studied the morphology of both staminate and pistillate spikelets and florets of maize, and compared it with that of related grasses in the tribes Maydeae and Andropogoneae. They found that the normal staminate spikelet of maize consists of two sterile glumes, the outer and inner ones (or the lower and upper ones) enclosing two flowers, and that the flowers consist of the flowering glumes, a lemma and a palea, two lodicules, and three stamens.

As several students of maize have pointed out, there are significant differences in the spikelets which are characteristic for each variety or group of closely related varieties. One of these characters is the morphology of the lower glume, which, combined with other characters, is useful for the recognition and description of maize varieties and races, as pointed out by Anderson and Cutler (1942).

MATERIAL AND METHODS

The material used in this study is mostly from Dr. Edgar Anderson's large collection of maize specimens from different parts of the world. Much of it was collected from cultivated fields, while a part was grown outside its original range in experimental plots. The Northern Flint varieties are partly from the Pioneer Hi-Bred Corn Company's herbarium at Johnston, Iowa. Five varieties of Bolivian corn are from Dr. Hugh Cutler's collection at the Chicago Natural History Museum. The prehistoric material from Arica, Chile, has been placed at my disposal by Mr. Junius Bird of the American Museum of Natural History, and that from Bat Cave, New Mexico, by Dr. Paul C. Mangelsdorf of the Botanical Museum of Harvard University. The author is indebted to all these individuals and organizations for the tassel specimens which they so kindly supplied and without which this study would have been impossible.

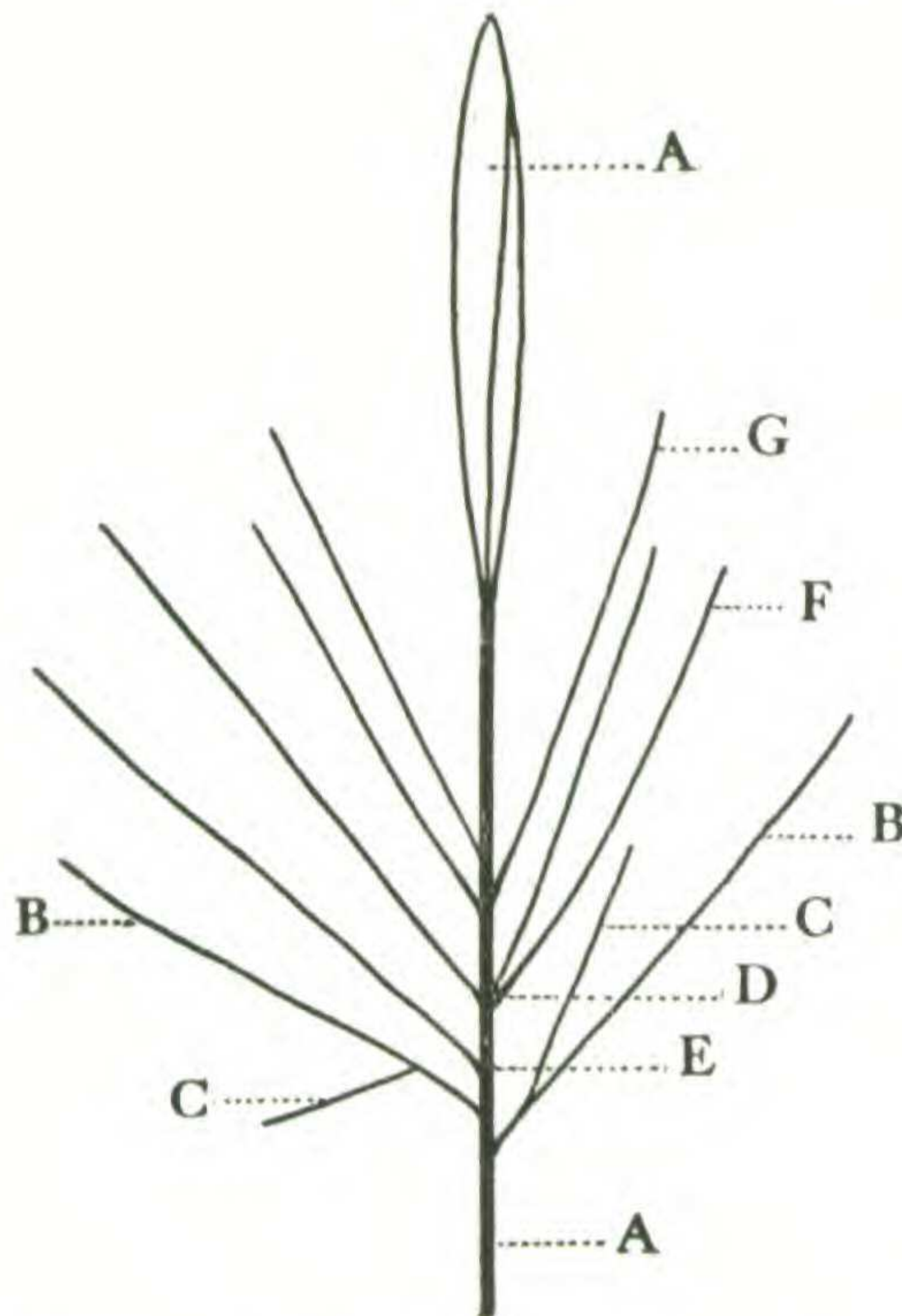


Fig. 1. Diagrammatic drawing of an average maize tassel: A, central spike; B, F, G, secondary branches; C, tertiary branches; D, whorl of secondary branches; E, a single secondary branch.

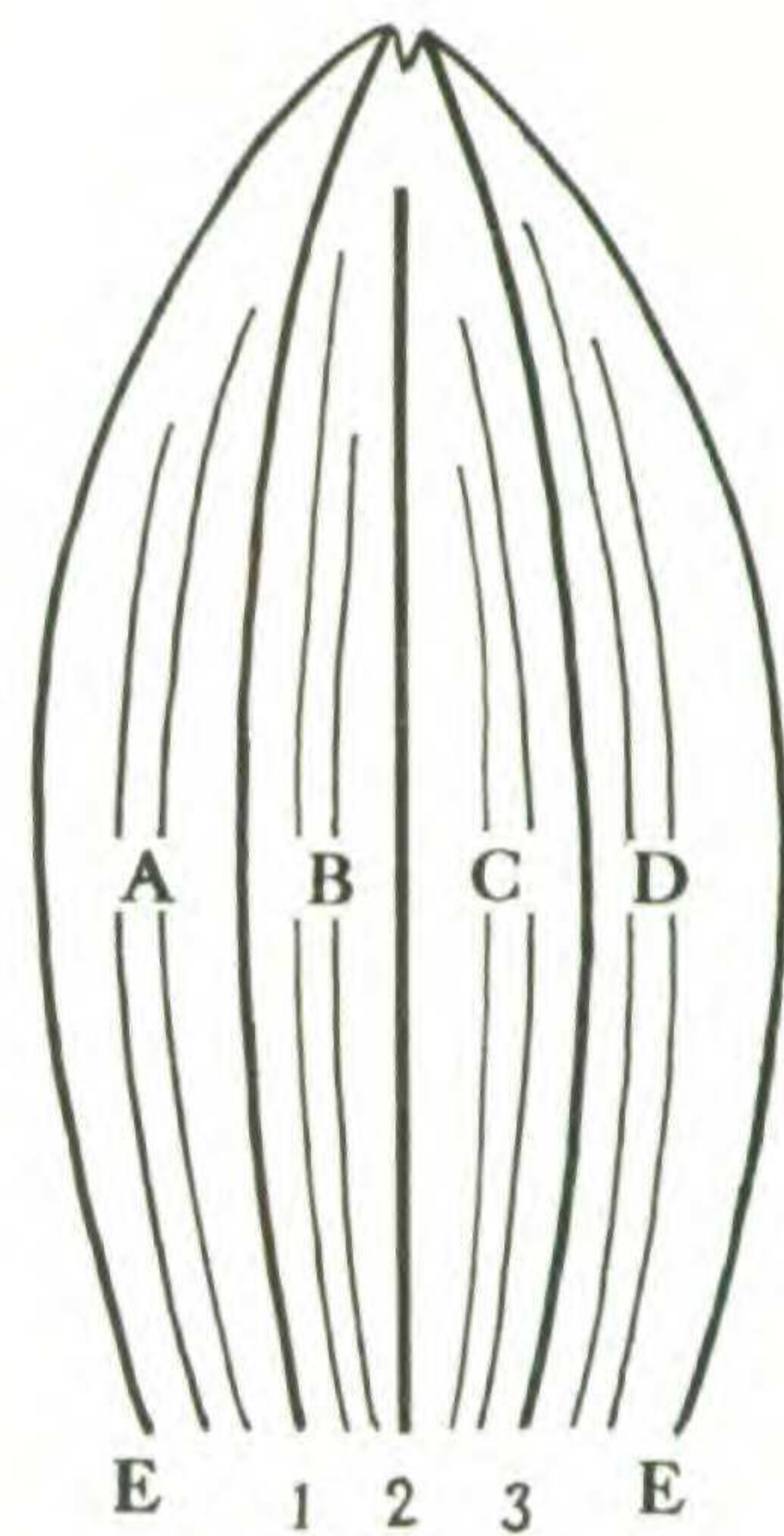


Fig. 2. Semi-diagrammatic glume from a staminate spikelet: 1, 3, keel veins; 2, median vein; A, left margin; B, left shoulder; C, right shoulder; D, right margin; E, edge of glume.

Since a certain variation exists between spikelets in an individual corn tassel, one has to be careful not to confuse this variation *within a plant* with the variation *between plants*. He has always to be sure that the material studied is taken from the same part of the tassel. In the present study this principle has been followed as completely as was possible.

In his study of prehistoric corn tassels from southern Utah, Anderson (1944c) described the general structure of an average corn tassel. His description, which gives a clear picture of the different parts of the male inflorescence and also explains the terminology most commonly used, refers to fig. 1:

The maize tassel is built upon a primary axis terminated by the CENTRAL SPIKE (A, fig. 1), along which the spikelets are arranged in many rows (in some South American varieties they are in whorls of 3 or more). Below the central spike are the SECONDARY BRANCHES 'B', 'F', 'G' whose number varies greatly in different races of maize. The lowermost secondaries may bear TERTIARY BRANCHES 'C', and in some South American varieties these may even produce branches of the fourth order. The secondaries may arise singly from the main axis (E) or may be in WHORLS (D) of two or more. On the secondaries the SPIKELETS are arranged in pairs, though, as will be shown below, there are departures from this regular arrangement in North American maize. In each pair one spikelet is ordinarily pedicellate and one is sessile, but in North America the pedicellate spikelet may be so subsessile as to be indistinguishable from its neighbor. In South American maize the secondaries often have a long sterile zone at the base of the secondary branches which is without spikelets. In the Southwest and in Mexico this zone is short or is lacking altogether.

In studying the spikelet characters the pedicellate spikelets of the median third of the central spike have been used whenever possible. An exception was the material from Bat Cave, which consisted of fragments of tassels alone, and only a few of these were from the central spike. Here the most representative and most characteristic spikelets were chosen for measurement.

In the glume, especially the lower one, the keel veins and the median vein are more prominent than the others and divide the glume into four distinctive areas (text-fig. 2). To facilitate description these areas have been named *left margin*, *left shoulder*, *right shoulder*, and *right margin*. The *shoulder* (B and C) is that part of the glume between the keel veins and is divided by the median vein into two parts, the left shoulder and the right shoulder. The *margin* (A and D) is that part of the glume between the edge of the glume and the keel vein. The veins in the margin are called *marginal veins* and those in the shoulder, *shoulder veins*.

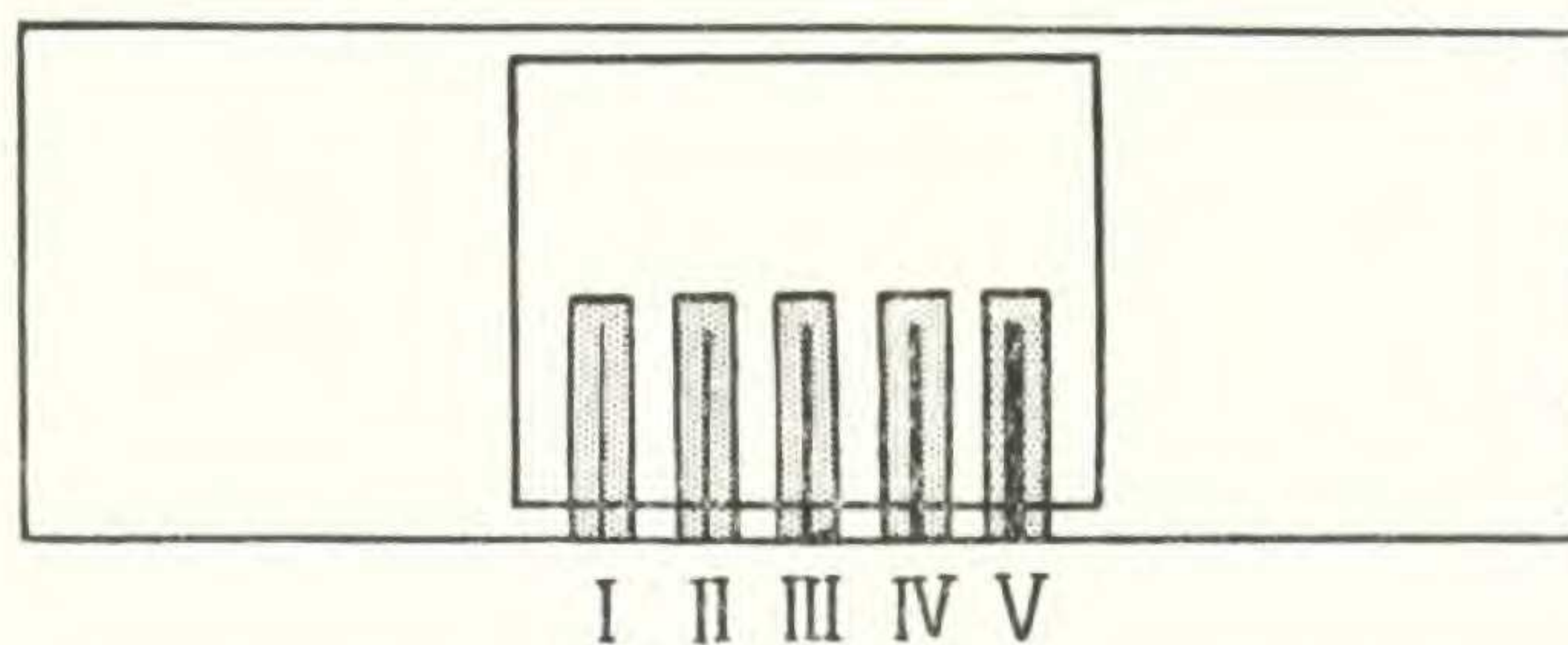


Fig. 3. Diagram of the microscope slide used in scoring the size of the veins in the glumes. When the size of the vein which is to be scored is smaller than I on the standard slide it is designated as O; veins which are as large as I, but smaller than II, are scored as I, and those as large as II but smaller than III are scored as II, etc. Veins as large as V or larger are scored as V.

In order to score the size of the veins, small pieces of glumes containing veins of different sizes were mounted in balsam on the edge of a microscope slide (text-fig. 3). Using this slide as a scale it was possible to classify the veins into six different categories, scored 0 to V inclusive. For the method of scoring see caption of text-fig. 3. The lower glumes from 20 pedicellate spikelets of each variety were measured and scored, using a dissecting microscope with an ocular micrometer. For each glume the following measurements were taken: the lengths of the glume and the median vein, the widths of the left and right margins, and those of the left and right shoulders, the number and sizes of all the veins. It being assumed that it was the averages of the margin widths and of the shoulder widths which were significant, these were computed for each glume measured. Arithmetic means of the measurements for each variety were then made and used in constructing the charts and diagrammatic drawings.

EXPLANATION OF PLATES 2-5

Semi-diagrammatic drawings of average glumes.

Twenty glumes of each variety were measured and scored and the mean values of the results calculated as outlined in the chapter on "Material and Methods." Since the resulting numbers referred chiefly to size, a representative glume most nearly meeting these average measurements was chosen to serve as a pattern for the shape. The drawings were made to the scale 1:15 and were later reduced to one-fifth size.

In each figure (from 1 to 114) the drawing to the left represents the glume shoulder and the one to the right, the right margin of the glume. The differences in vein size are indicated by different widths of lines. For example, in fig. 1, drawing to the left, the sizes of the veins are, from left to right, 3, 1, 0, 2, 0, 1, 3, and in the drawing to the right, 3, 0, 1, 1; and in fig. 13, drawing to the left, the sizes of the veins are 5, 2, 2, 3, 2, 2, 5, and in the one to the right, 5, 2, 3, 2. The number and sizes of the veins, as well as the other measurements, are given in the table in Appendix II.

The drawings on plates 2-5 represent the following varieties:

PLATE 2

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| 1. Arica, Quiani Excavation, Division I, Layer D 1 | 13. Burma |
| 2. Arica, Playa Miller Excavation, Level ABC | 14. India |
| 3. Arica, Playa Miller Excavation, Level D 3, No. 1 | 15. Siam |
| 4. Arica, Playa Miller Excavation, Level D 3, No. 2 | 16. Assam #1074 |
| 5. Bat Cave, VI-128 | 17. Assam #44 |
| 6. Bat Cave, IV-329-1 | 18. Chinese Waxy |
| 7. Bat Cave, IV-280 | 19. China #149114A |
| 8. Bat Cave, IV-329-2 | 20. China #149118 |
| 9. Bat Cave, V-186 | 21. Argentine Popcorn |
| 10. Bat Cave, IV-329-3 | 22. Río Loa |
| 11. Bat Cave, IV-301-2 | 23. Soledad #5065-2 |
| 12. Turkey | 24. Soledad #5075-3 |
| | 25. Soledad #5075-5 |
| | 26. Soledad #5075-1 |
| | 27. Creole Flint |

PLATE 3

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|------------------------------------|---------------------------------|
| 28. Bolivia, Mangelsdorf's #127895 | 40. Cuzco #10-2 |
| 29. Coroico #6094-2 | 41. Cuzco #9-2 |
| 30. Valle #6165 | 42. Cuzco #8-9 |
| 31. Titicaca #7700-5 | 43. Cuzco #4-3 |
| 32. Titicaca #7729-2 | 44. Cuzco #3-1 |
| 33. Titicaca #7729-5 | 45. Maíz reventador, Coalcomán |
| 34. Manglaralto | 46. Sa 15 b-4 |
| 35. Quito #8-4 | 47. Maíz chapolote |
| 36. Quito #1-6 | 48. Talpa |
| 37. Quito #9-3 | 49. Culiacán #1-8 |
| 38. Quito #4-2 | 50. Sauer #11-4 |
| 39. Quito #6-1 | 51. Maíz reventador, Kelly #3-4 |

PLATE 4

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|-------------------------------|-----------------------------|
| 52. Hackberry | 63. Early Quebec Flint |
| 53. Elberta | 64. Parker's Flint #1 |
| 54. Hickory King | 65. Parker's Flint #2 |
| 55. Latham's Double | 66. 14-row Dakota Flint |
| 56. Knighton Little Cob Flint | 67. Longfellow #1 |
| 57. Louisiana Gourdseed | 68. Stevens Flint |
| 58. Tennessee Red Cob | 69. Longfellow #2 |
| 59. Mandan Yellow Flour | 70. Tama Flour Corn #1 |
| 60. Harris Mammoth Yellow | 71. Tama Flour Corn #2 |
| 61. Fort Kent | 72. Cherokee Indian Corn #1 |
| 62. Dryden | 73. Cherokee Indian Corn #2 |

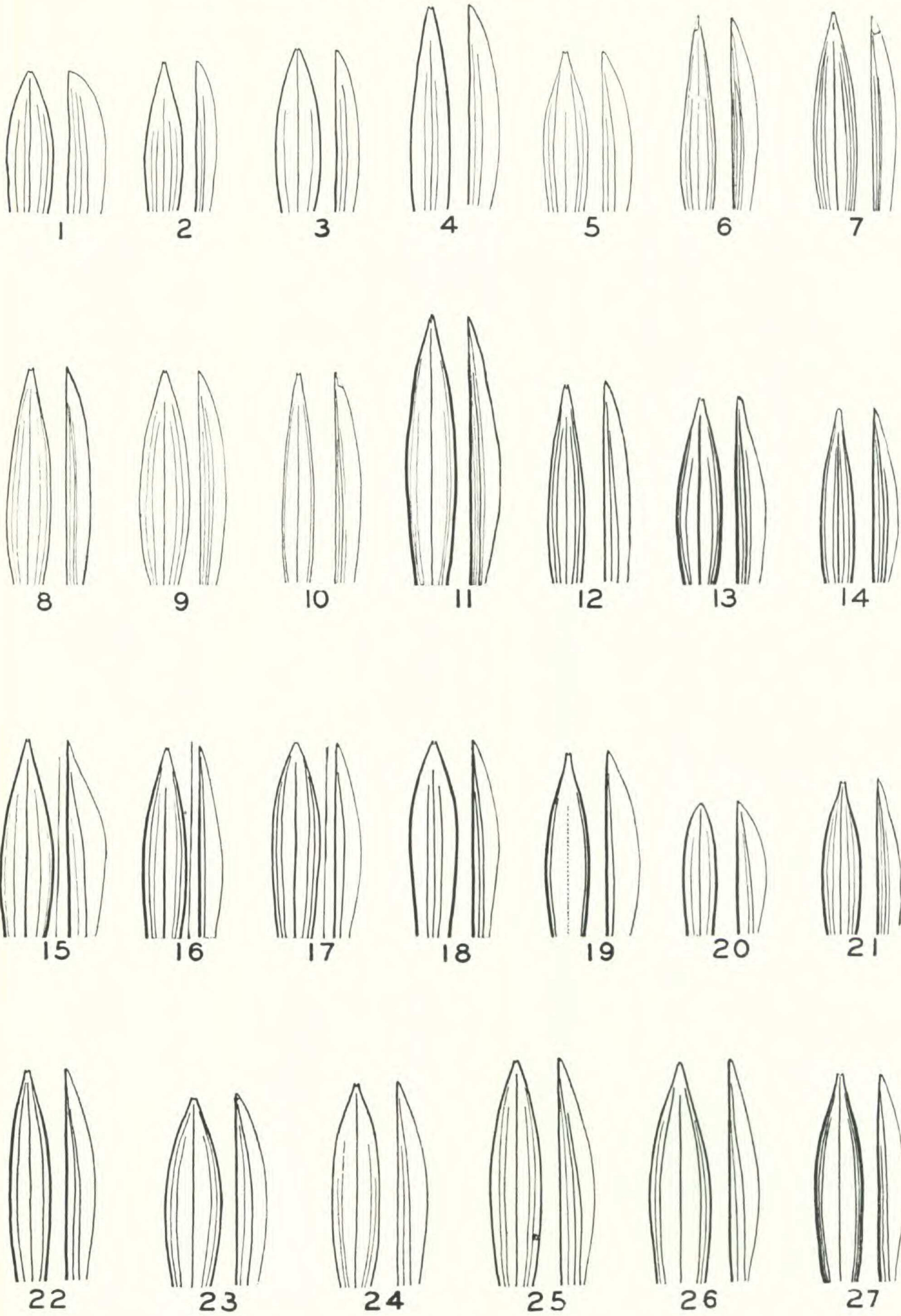


PLATE 2

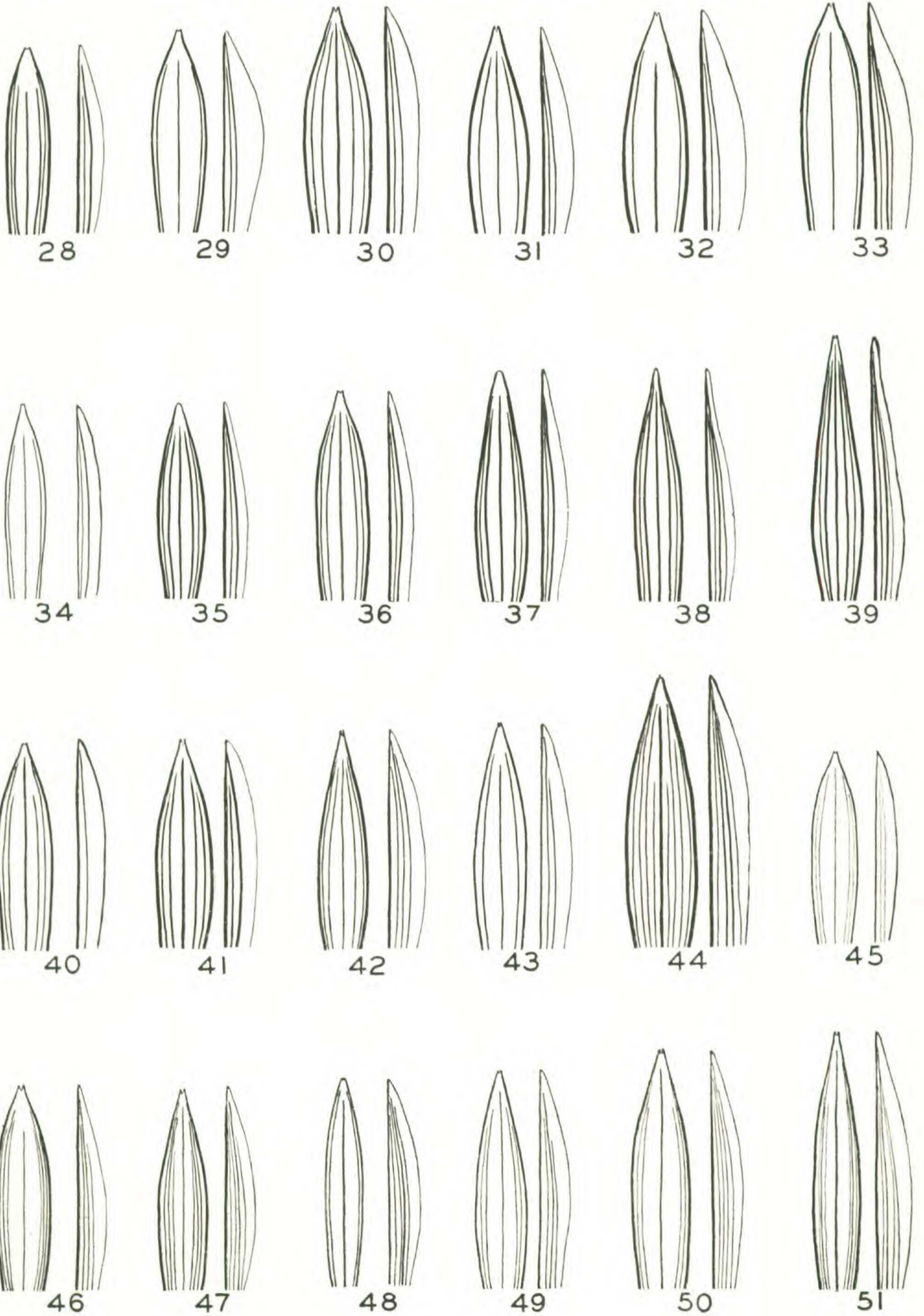


PLATE 3

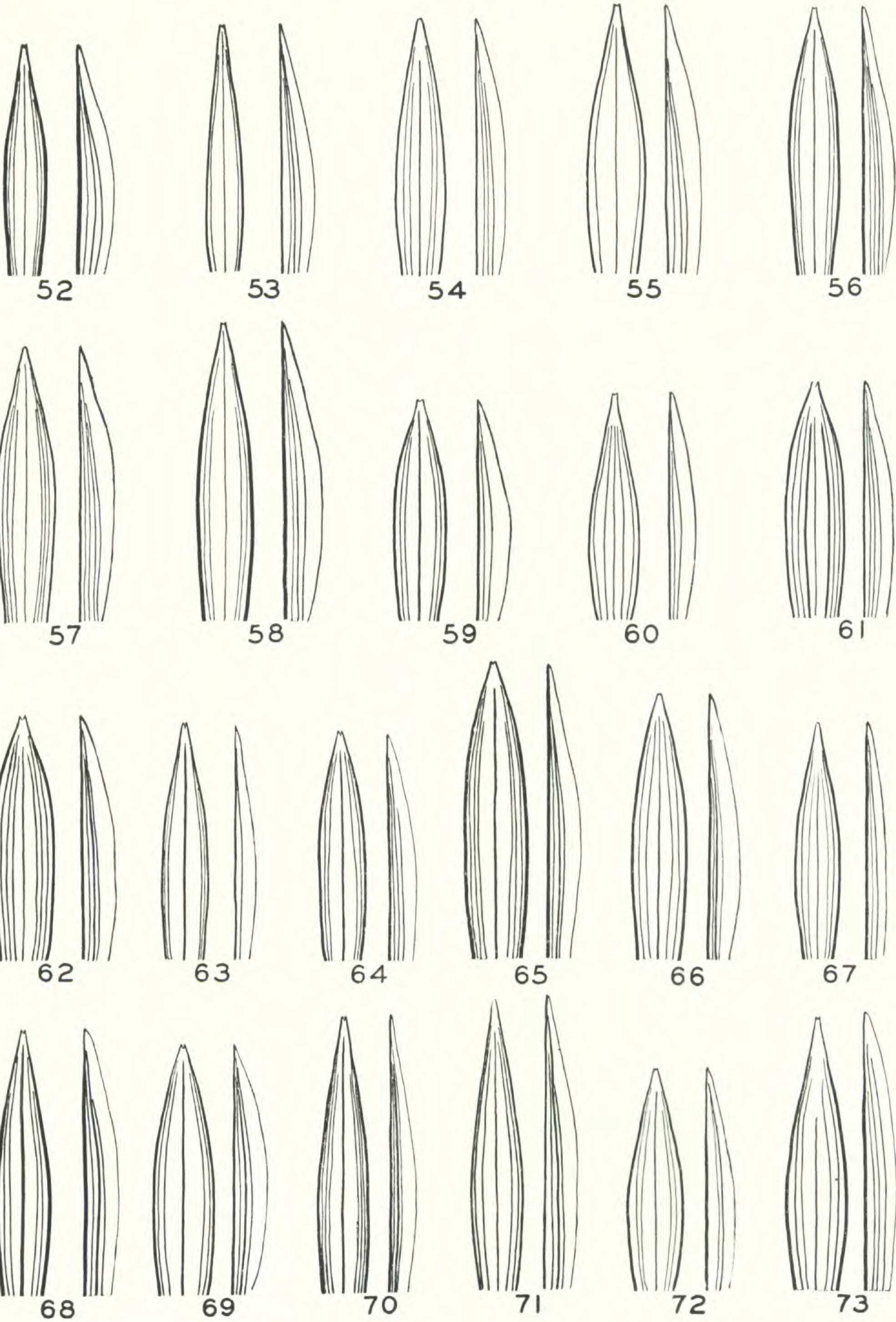


PLATE 4

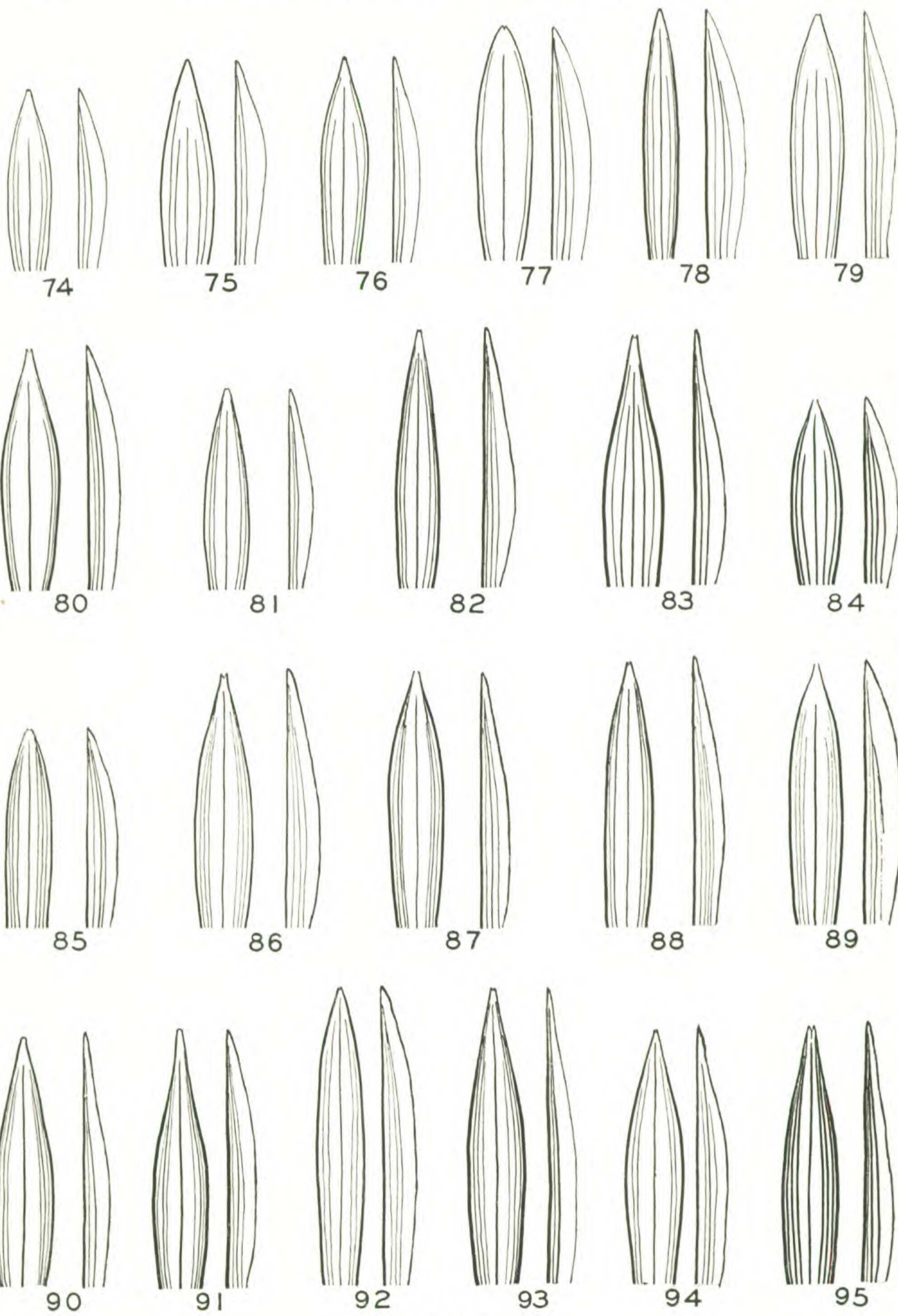


PLATE 5

All the material used in this study is divided into groups according either to geographical distribution or to the similarity of the varieties with respect to different characters. These groups are:

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|--|--|
| A. Prehistoric maize: | { 1. Arica 2. Bat Cave |
| B. South American maize: | { 1. Old South American Pop Corn 2. Andean Highland maize |
| C. Central American and Mexican maize: | { 1. Western Mexican maize 2. Maize from El Capulin and Toluca 3. Guatemalan maize |
| D. Caribbean maize: | { 1. Cuban maize 2. Creole Flint |
| E. North American maize: | { 1. Northern Flints 2. Papago maize 3. Southern Dents |
| F. Oriental maize: | { Varieties from Assam, Burma, China, India, Siam and Turkey |

The exact origin of all these collections is given in Appendix I.

PREHISTORIC TASSEL MATERIAL

For understanding variation in the spikelets of modern varieties of maize the discoveries of prehistoric tassels and tassel fragments are of great potential value. In order to understand what changes, if any, have taken place in the entire corn tassel through the centuries the tassels of ancient varieties furnish important objects for comparison. Of several museum collections of prehistoric and pre-Columbian maize tassels, the collection from Arica, Chile (Bird, 1943) and that from Bat Cave, New Mexico (Mangelsdorf and Smith, 1949) have not previously been investigated in detail.

Beginning in 1941, under the sponsorship of the Institute of Andean Research, extensive archeological excavations were made by Mr. Junius Bird at Arica in northern Chile. Among the rather abundant maize remains discovered were four complete and well-preserved tassels, which came from three different levels. The exact age of the deposits at Arica is not yet known but three major periods have been defined, one pottery period and two pre-pottery periods. The second pre-pottery period ended with the beginning of agriculture. Of the material used in this study one tassel, that of the Quiani Excavation, Division I, layer D 1, represents the oldest type; the three others are somewhat younger and are from levels D 3 and ABC of Playa Miller Excavation.

PLATE 5

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|-------------------------|-------------------------------|
| 74. Santa Lucia #3 | 85. San Andreas |
| 75. Santa Lucia #6 | 86. Coyote #1 |
| 76. Santa Lucia #4 | 87. Topawa #2 |
| 77. Santa Lucia #2 | 88. Topawa #1 |
| 78. Santa Lucia #1 | 89. Pia Oik #2 |
| 79. Santa Lucia #5 | 90. Kerwo #1 |
| 80. Maíz de Elote | 91. Kerwo #2 |
| 81. Toluca #2 | 92. Coyote #2 |
| 82. Toluca #1 | 93. Cold Fields #5 |
| 83. El Capulin #1063 | 94. Pia Oik #1 |
| 84. Chiripo Indian Corn | 95. Papago (Lochiel, Arizona) |

In 1948 an expedition from the Peabody Museum of Harvard University made excavations in Bat Cave, Catron County, New Mexico. According to Dr. Ernst Antevs, who determined the age of the material found in Bat Cave, "the cultural deposits containing the maize had their beginning not later than 2500 B. C." (Mangelsdorf and Smith, 1949, p. 217). Arnold and Libby (1951), using the radio-carbon technique, have determined the age of the oldest maize-bearing deposits, the depth of which is three to four feet, as being 2249 ± 250 years, and the age of the youngest deposits, which are up to one foot deep, as being 1752 ± 250 years. Mangelsdorf and Smith, using pottery as an index, had previously calculated that the deposits containing maize remains covered a total span of not less than 3000 years. The radio-carbon technique has, however, shown that the span is probably less than that, the difference in age between the oldest and youngest maize-bearing levels being only 500–1000 years.

The depth of the deposits in Bat Cave in which maize remains have been found averaged between five and six feet. The lowest level, or stratum, was designated as I, and the uppermost as VI (Mangelsdorf and Smith, 1949). Altogether, eight tassel fragments and one rather complete tassel were found. All this material is from the three upper levels, IV, V, and VI. In level IV one tassel (#329-3), three fragments of central spikes (#301-2, #329-1 and #329-2) and two fragments of secondary branches (#301-1 and #280) were found. Level V contained one fragment of a central spike (#186) and a fragment of a lateral branch (#212). In level VI only a fragment of a lateral branch (#128) was found.

In both the Arica and the Bat Cave material the branching of the tassels, as well as the arrangement of the spikelets in the tassels and the fragments, was studied (pls. 7–9). The lengths of the internodes and of the pedicels of the spikelets were measured and are presented to scale as diagrammatic drawings. In the material from Arica the central spike or a portion of it and one or two secondary and tertiary branches (in each case the most characteristic ones for each variety) are represented in the detailed drawings (pls. 7–8). In the material from Bat Cave both the tassel and all the fragments are represented (pl. 9).

EXPLANATION OF PLATE 6

This plate compares variation within the same tassel with that between different tassels in the same field. The upper two rows of figures represent a relatively uniform variety, the lower two rows, an extremely variable one. Measurements, scoring, and construction of diagrams are described in "Explanation of Plates 2–5."

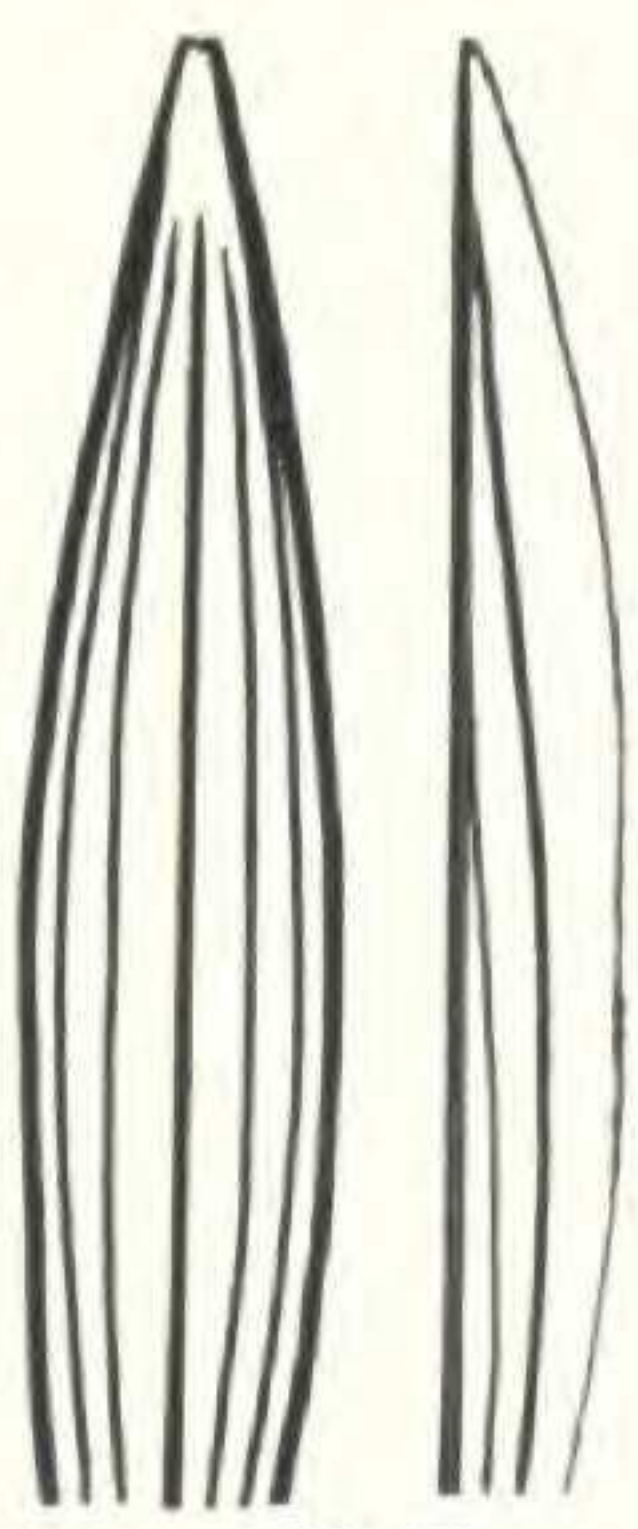
Figs. 96–100. Five individual spikelets from one plant of El Capulin #1059.

Figs. 101–105. Average spikelet of five different plants of El Capulin: fig. 101, #1062; fig. 102, #1059; fig. 103, #1064; fig. 104, #1062A; fig. 105, #1060.

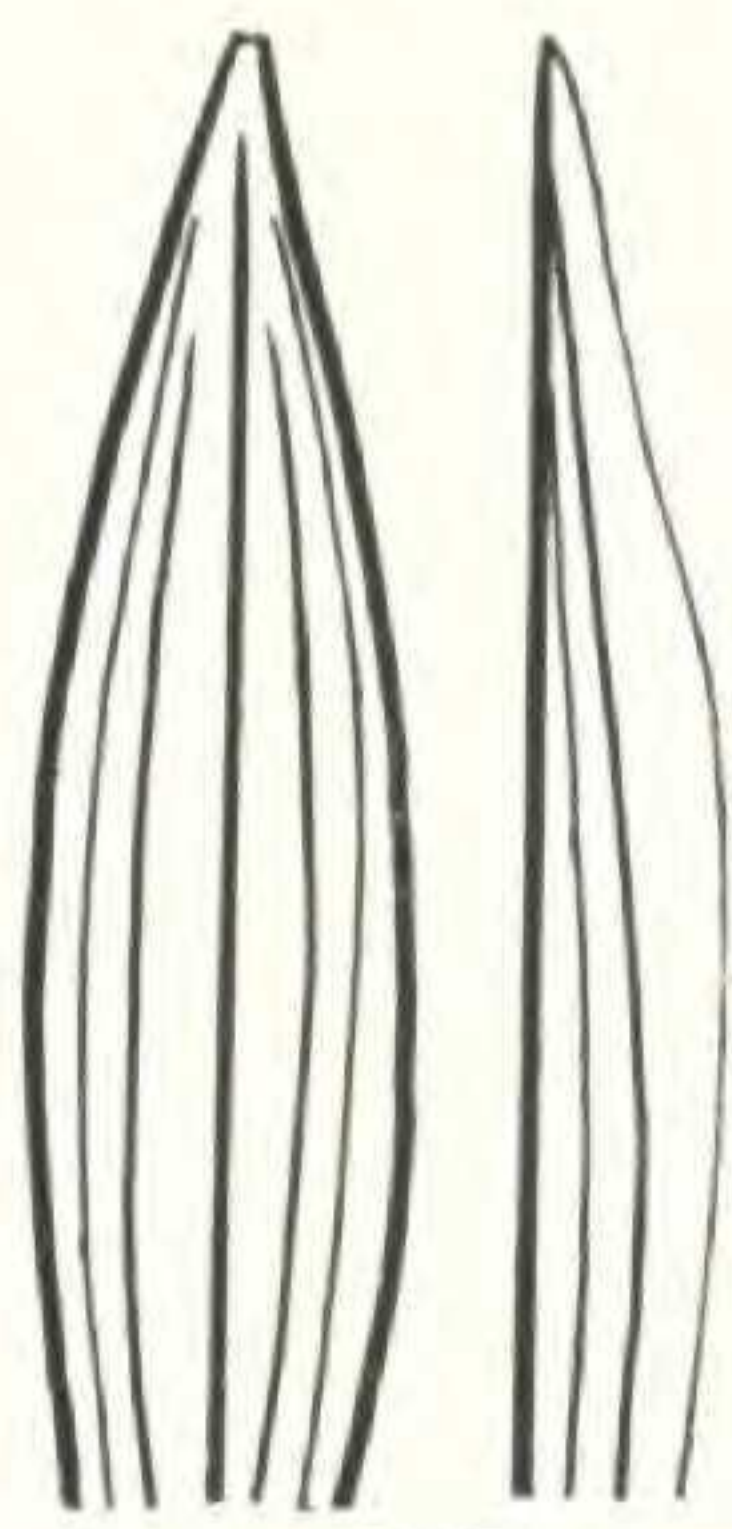
Figs. 106–110. Five individual spikelets of one plant of Papago maize, Chukut Kuk #1.

Figs. 111–114. Average spikelets from four different plants of Papago maize, Chukut Kuk: fig. 111, #1; fig. 112, #2; fig. 113, #3; fig. 114, #4.

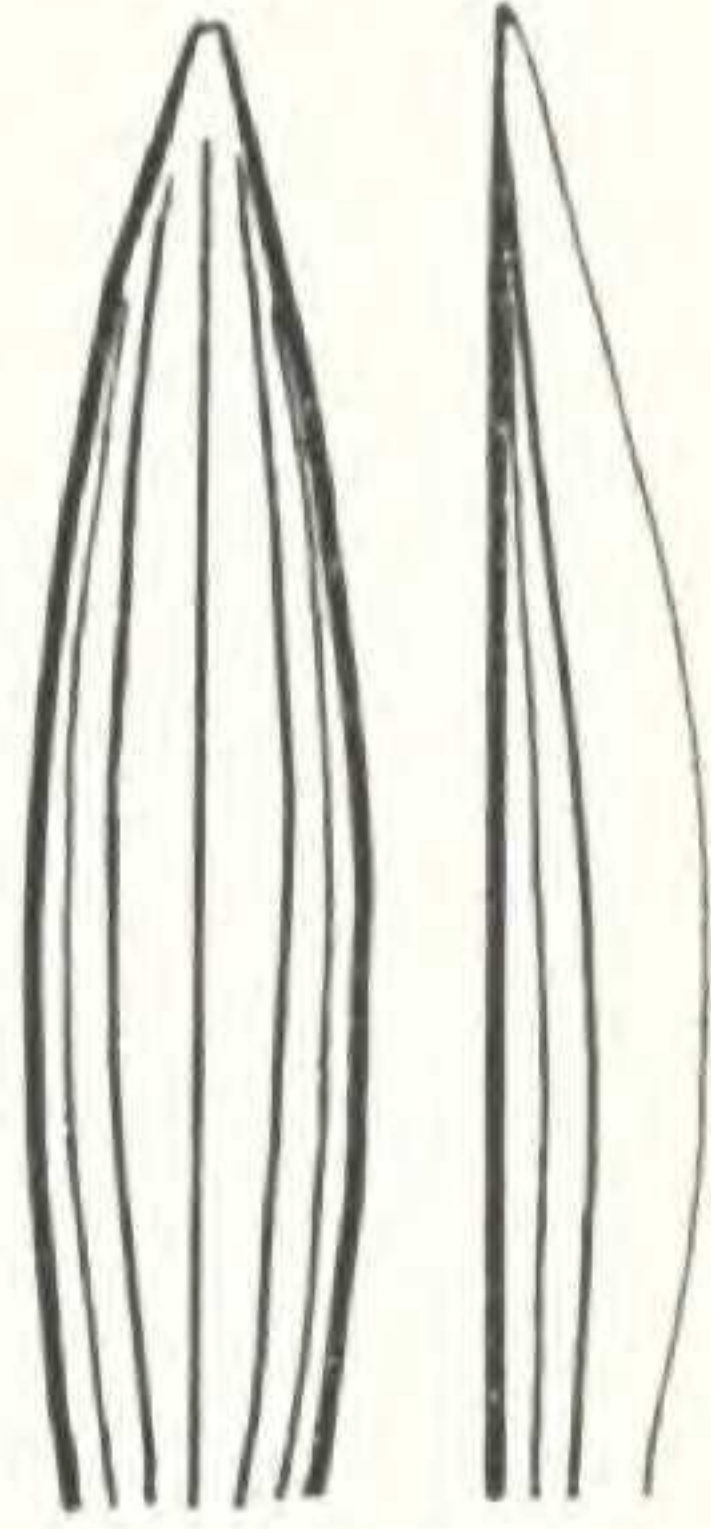
EL CAPULIN



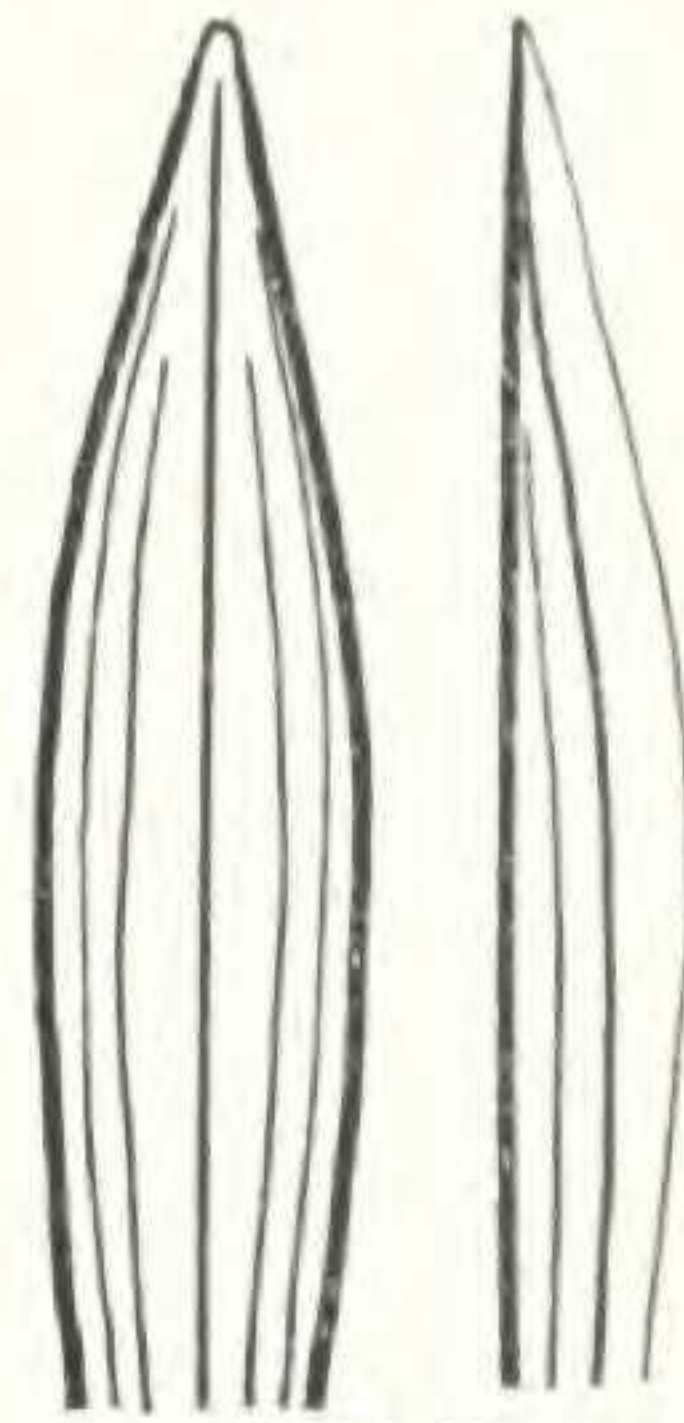
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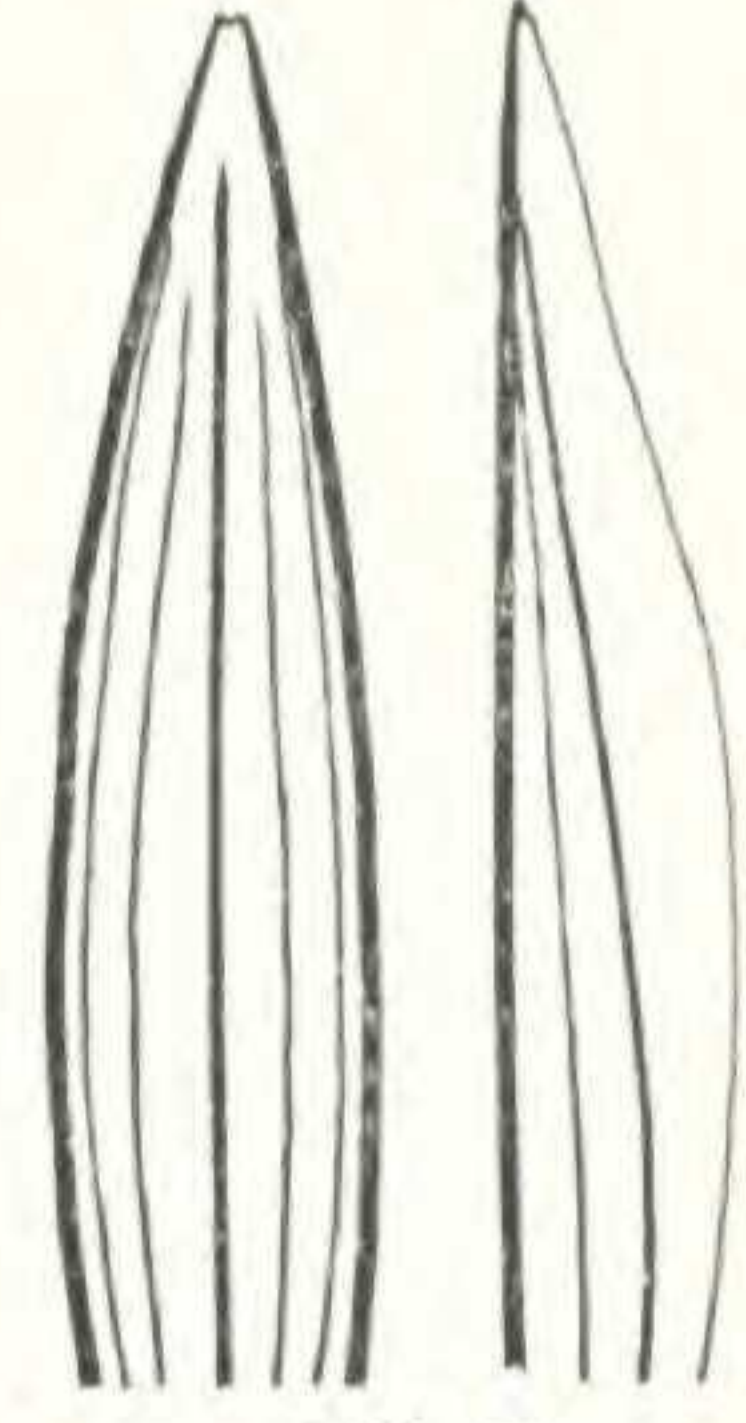
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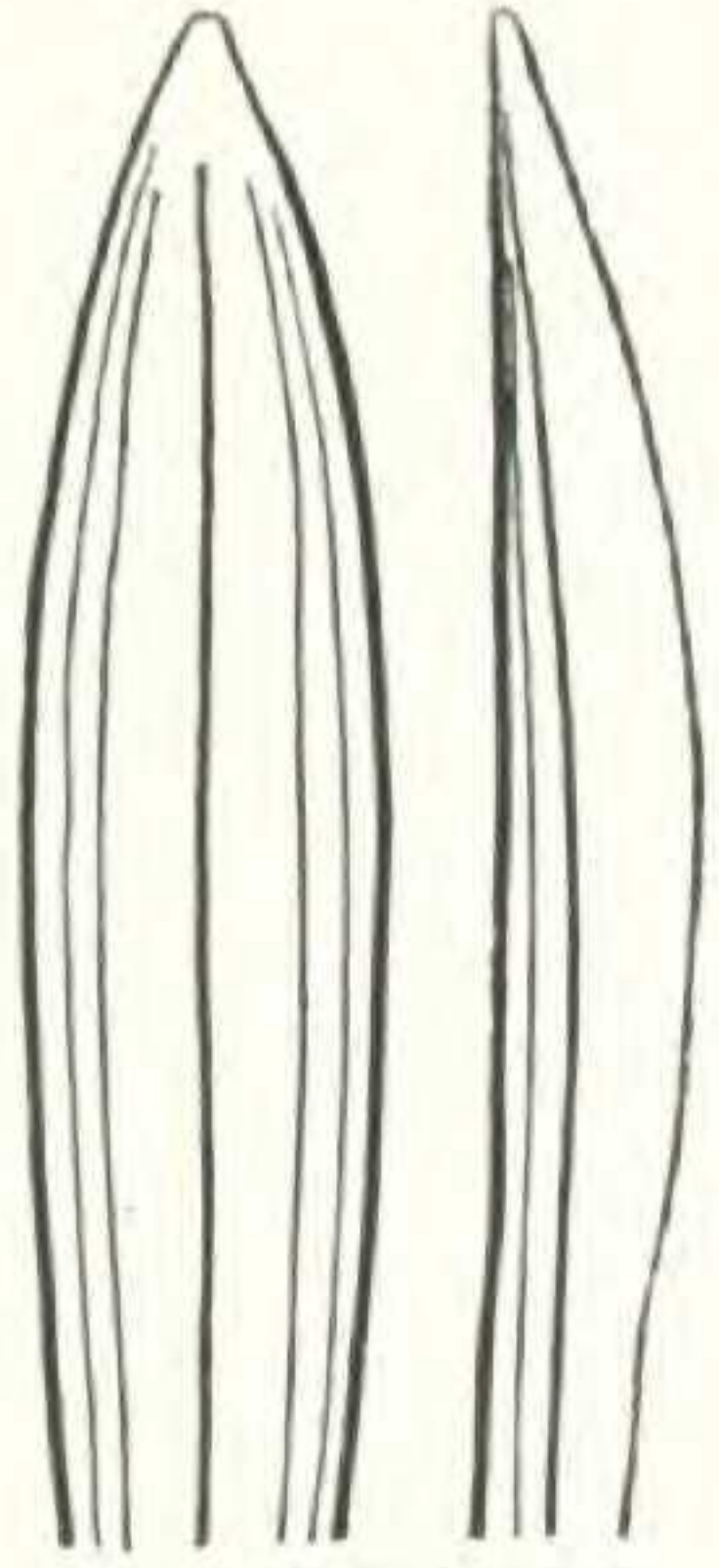
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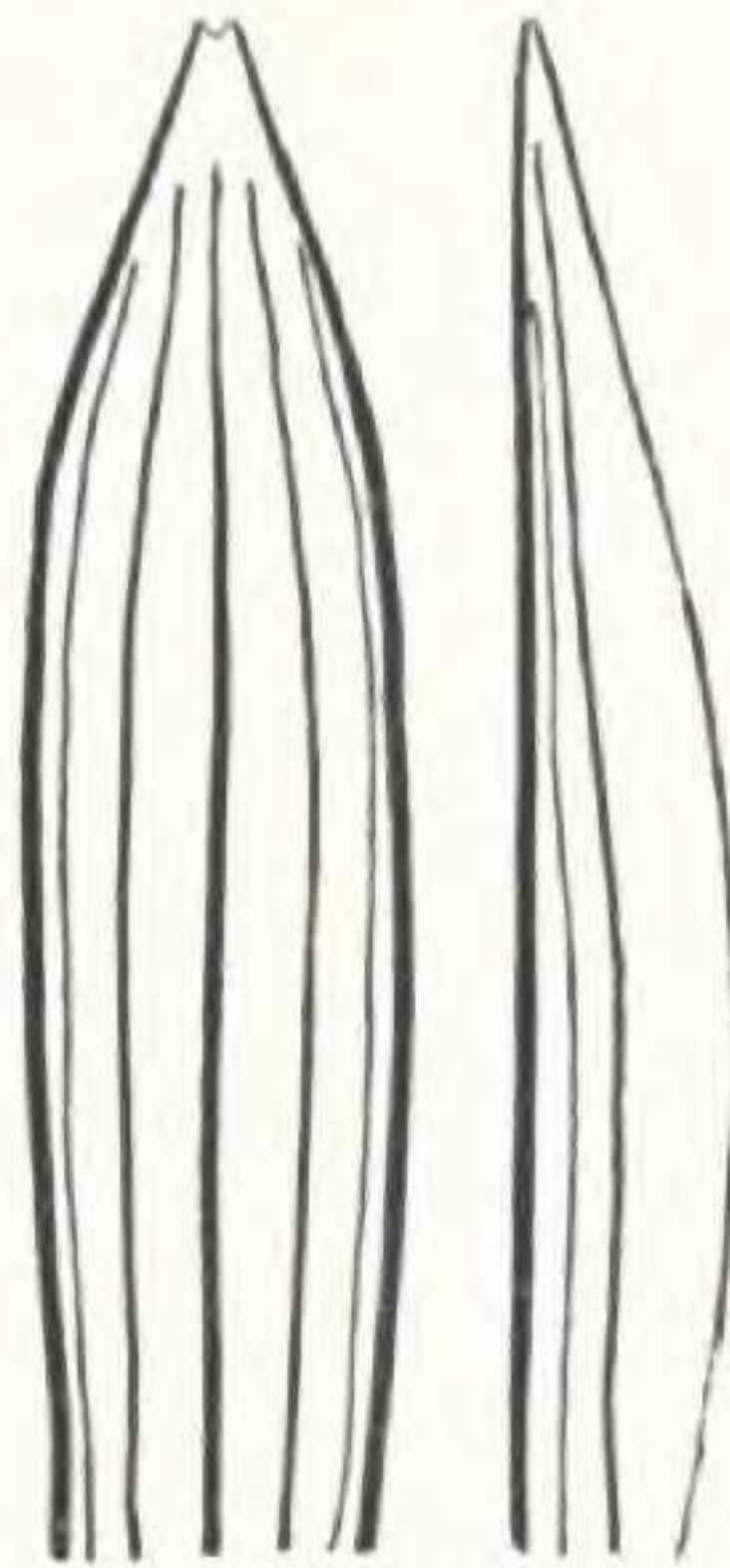
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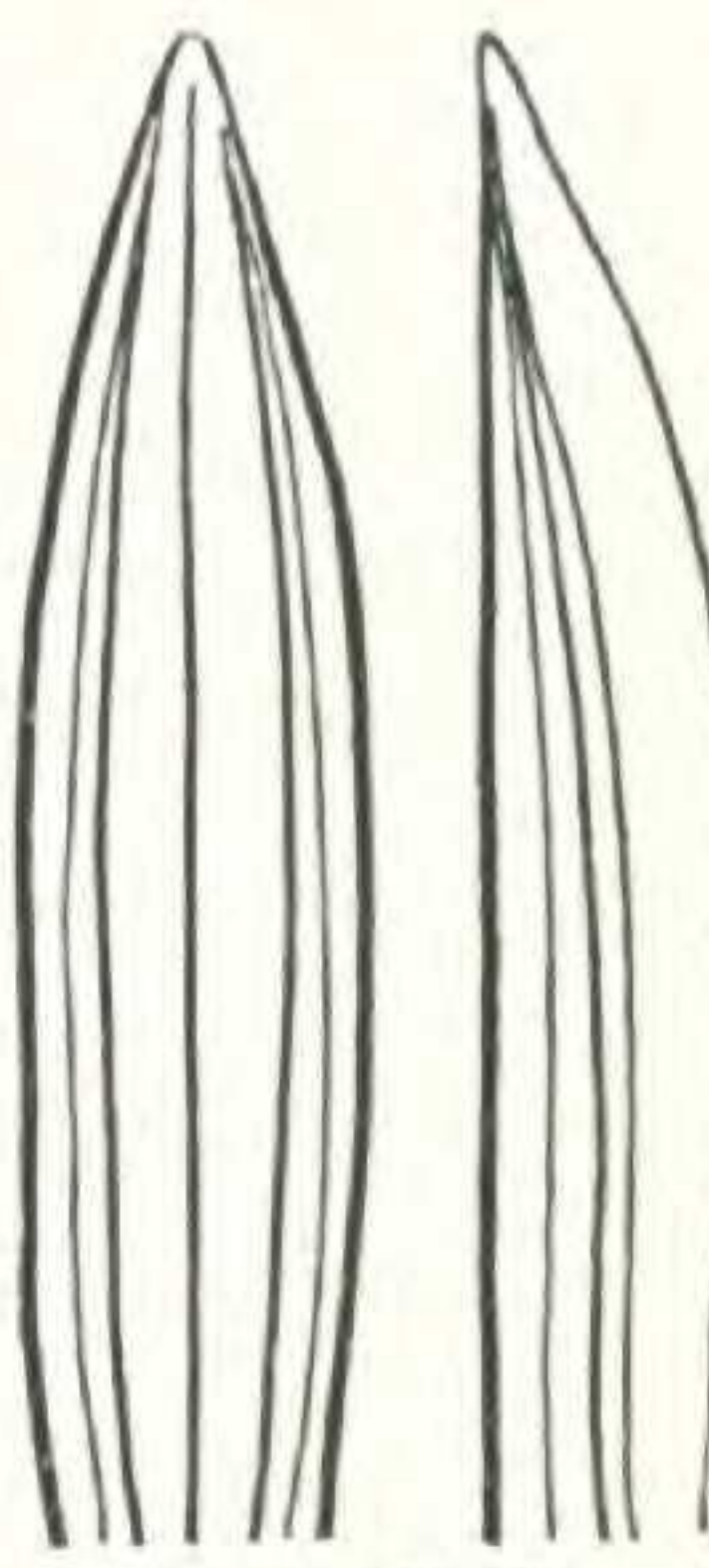
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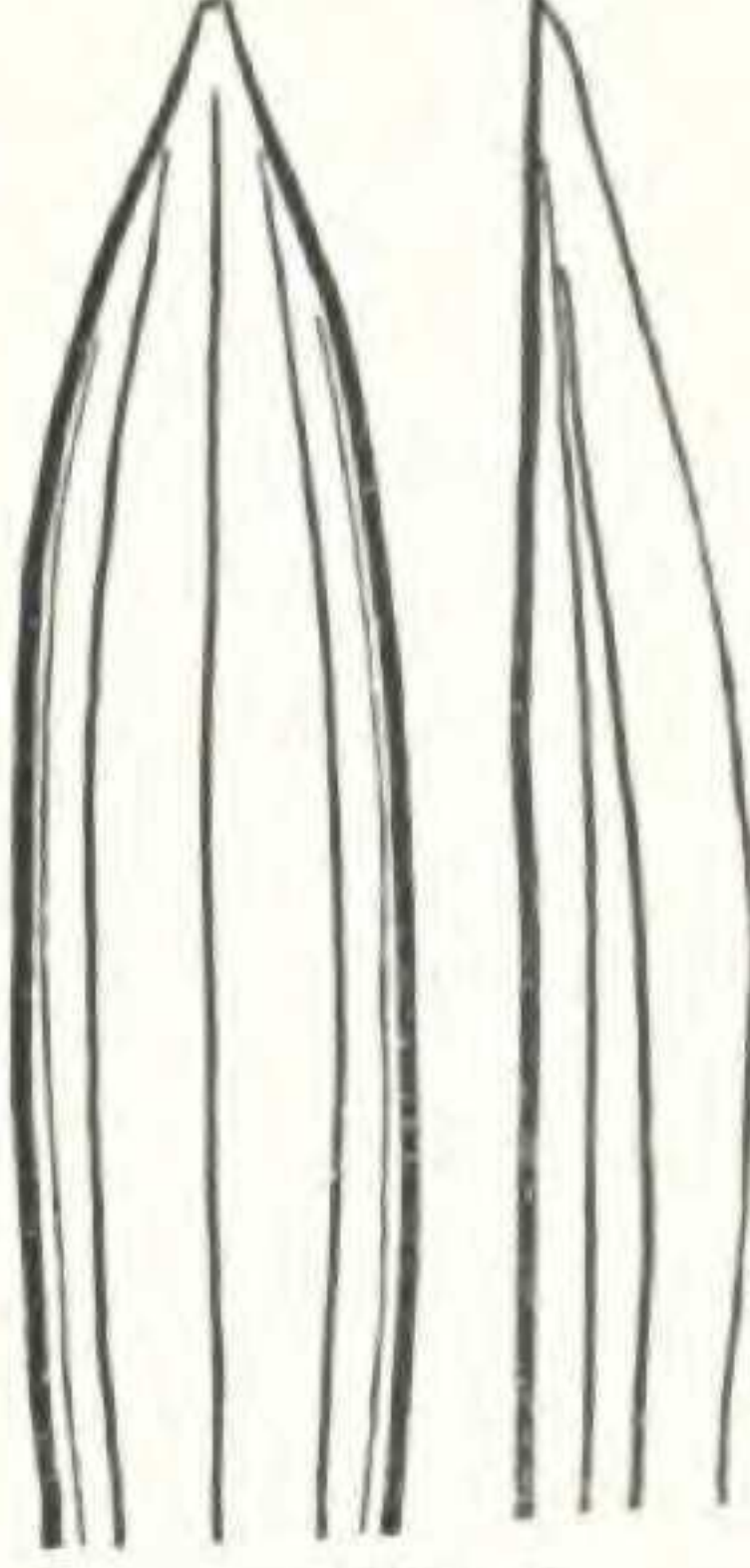
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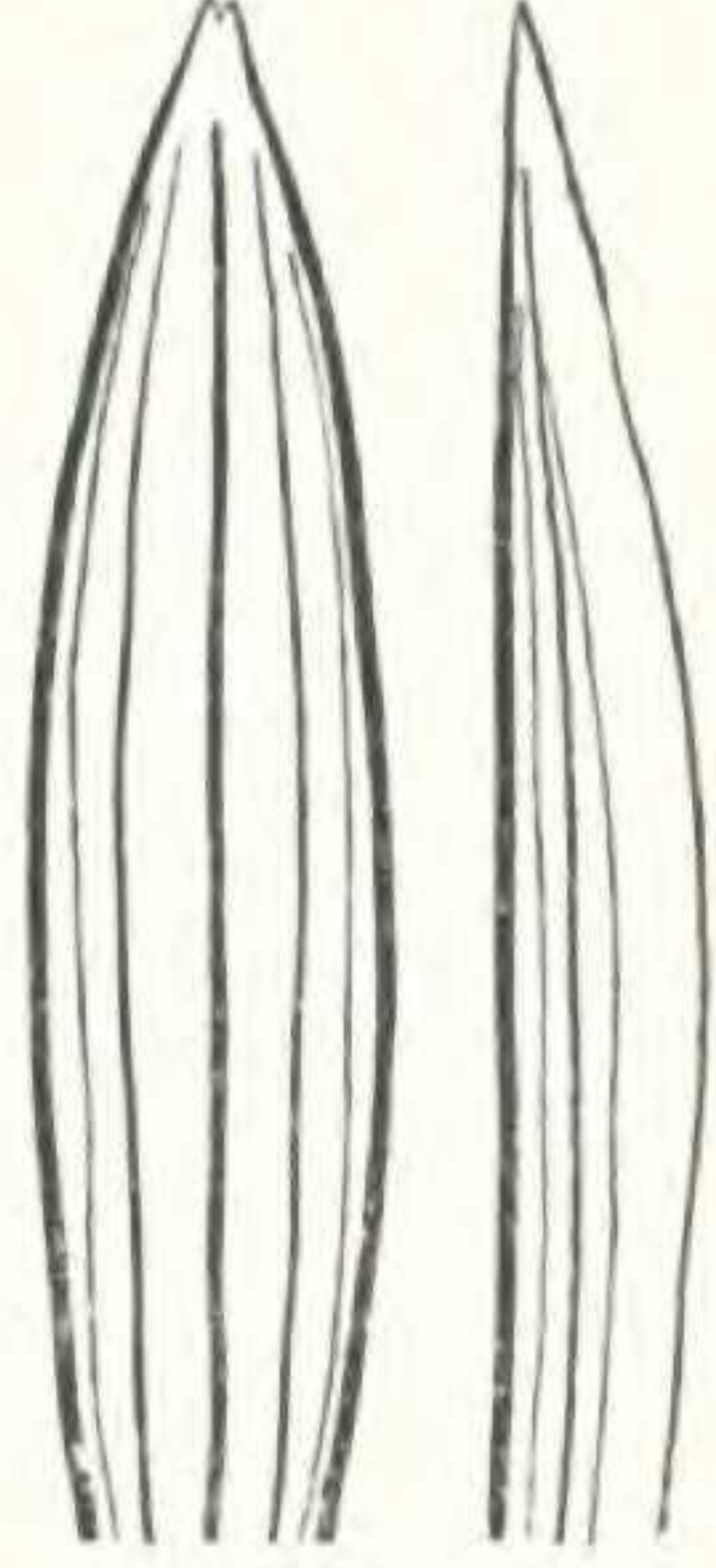
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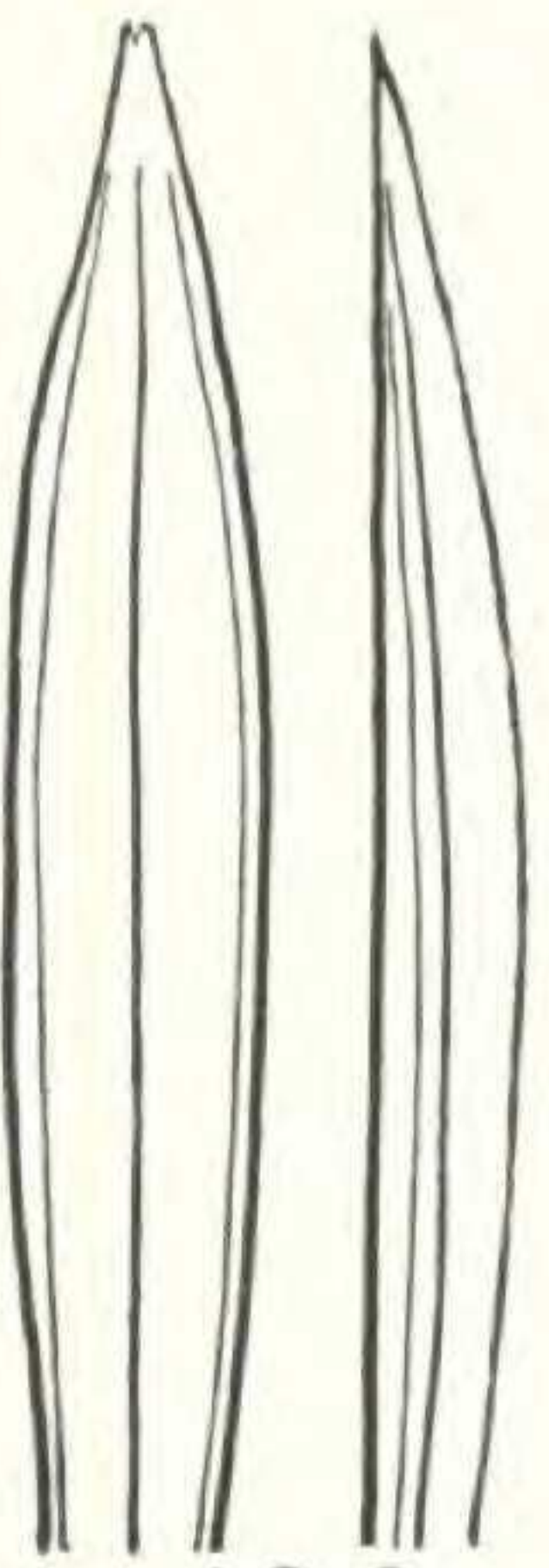


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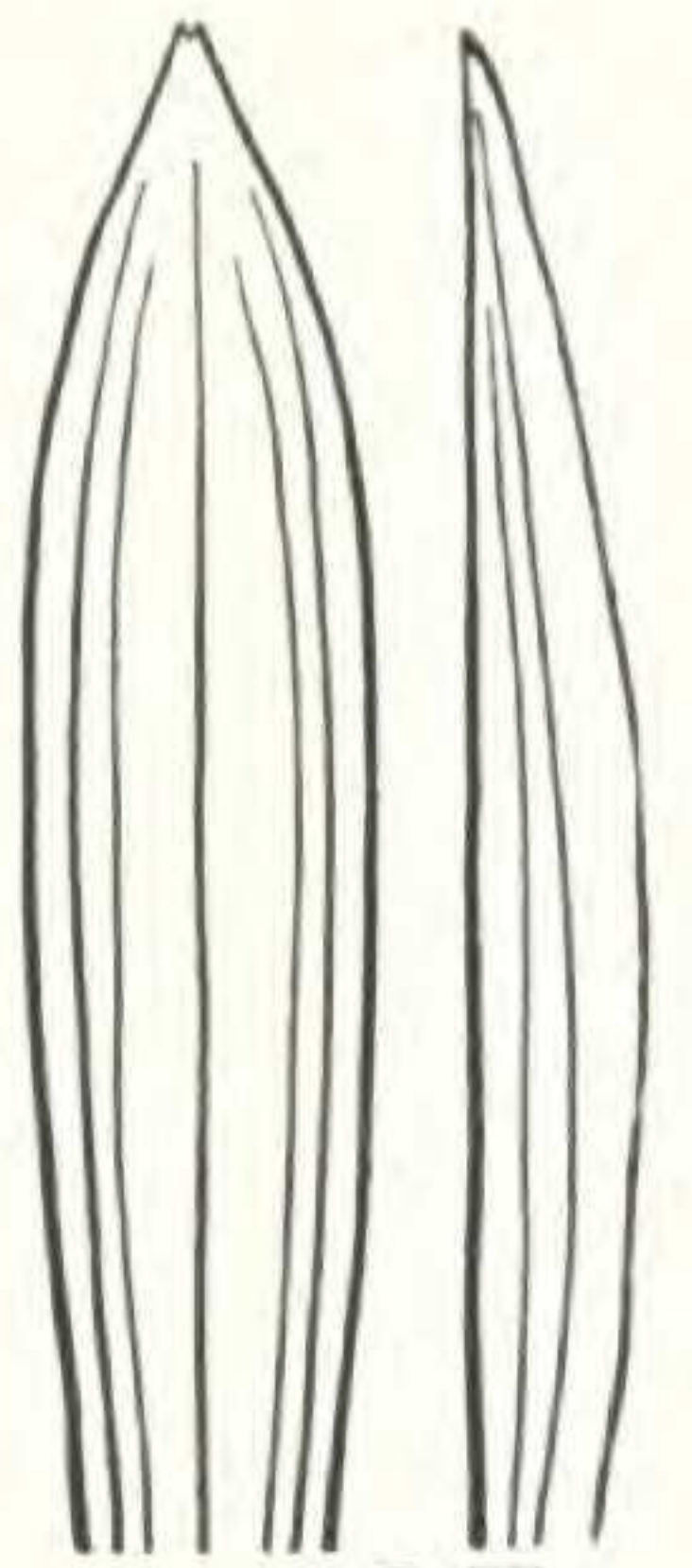


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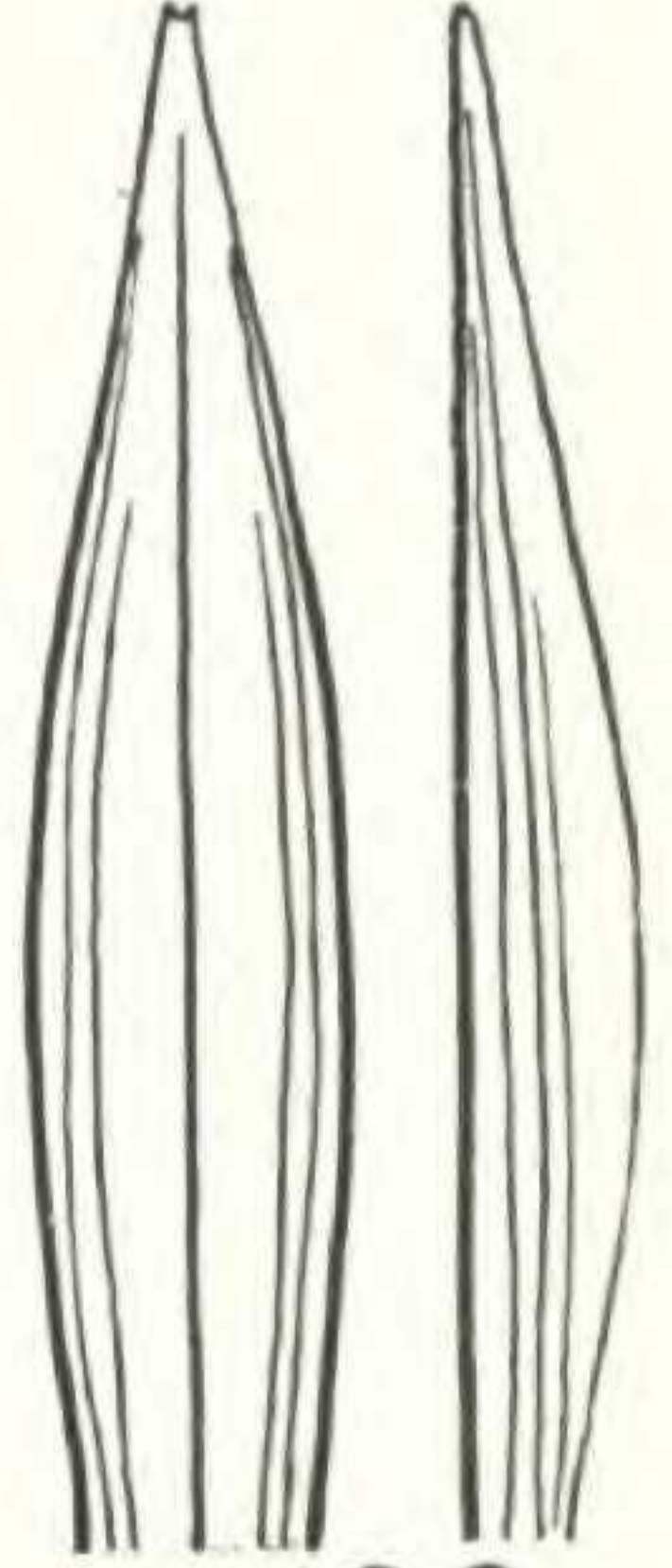
PAPAGO



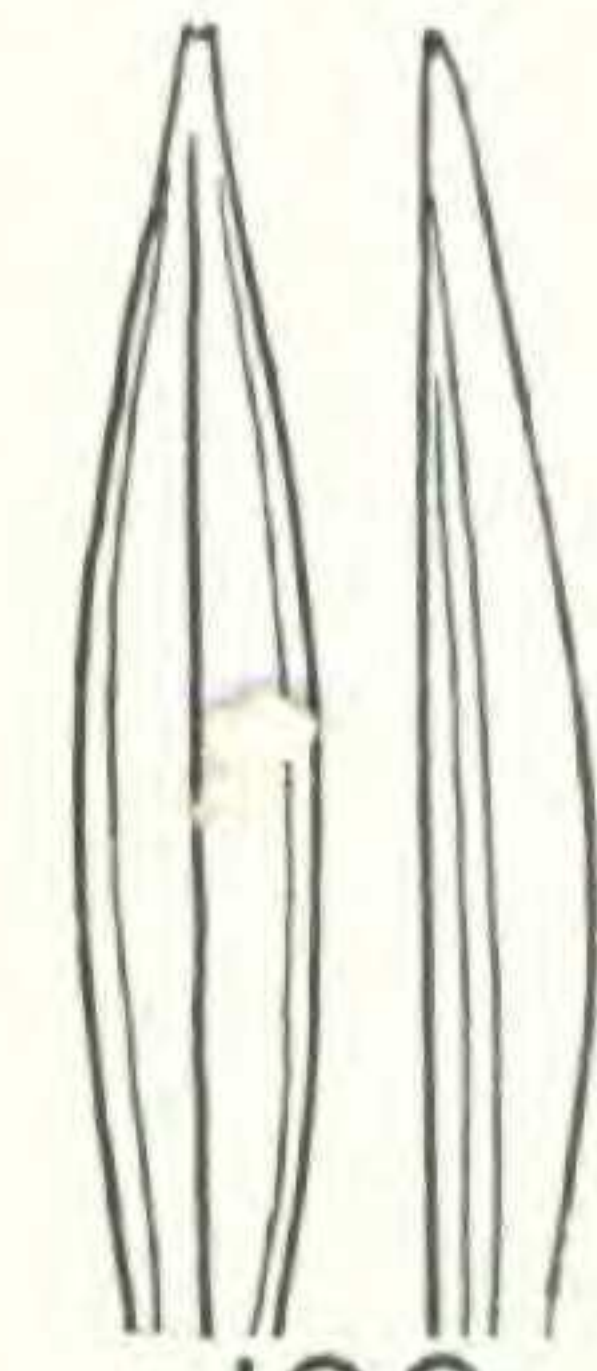
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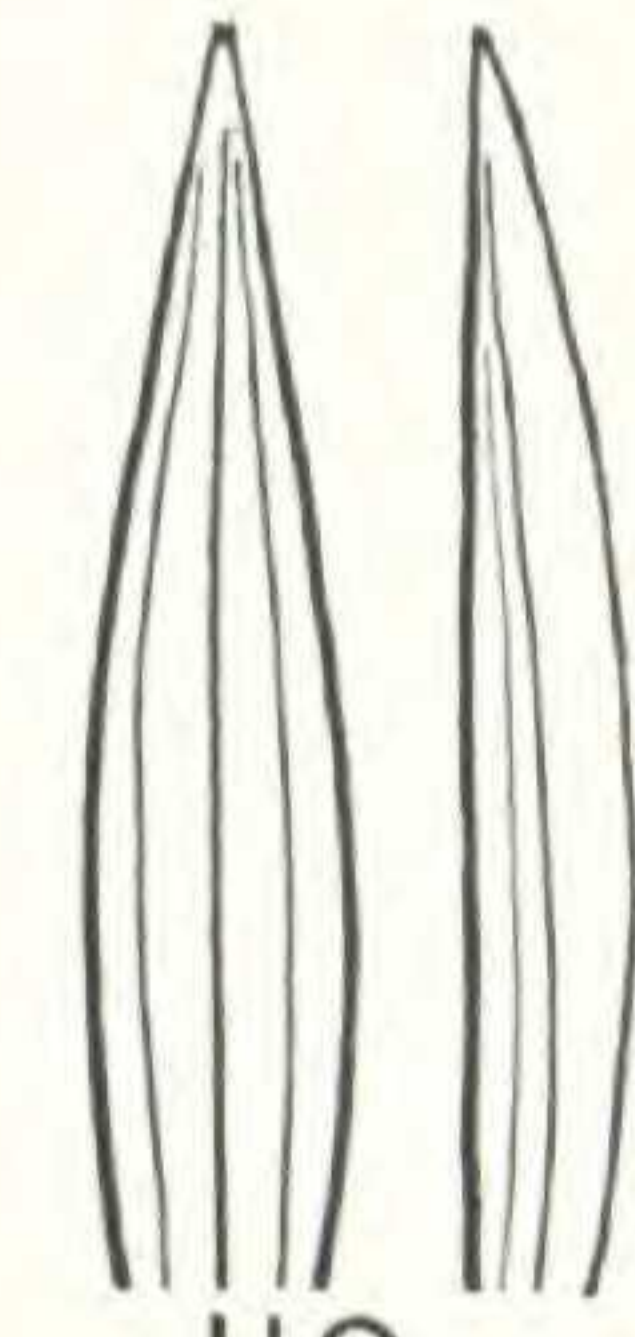
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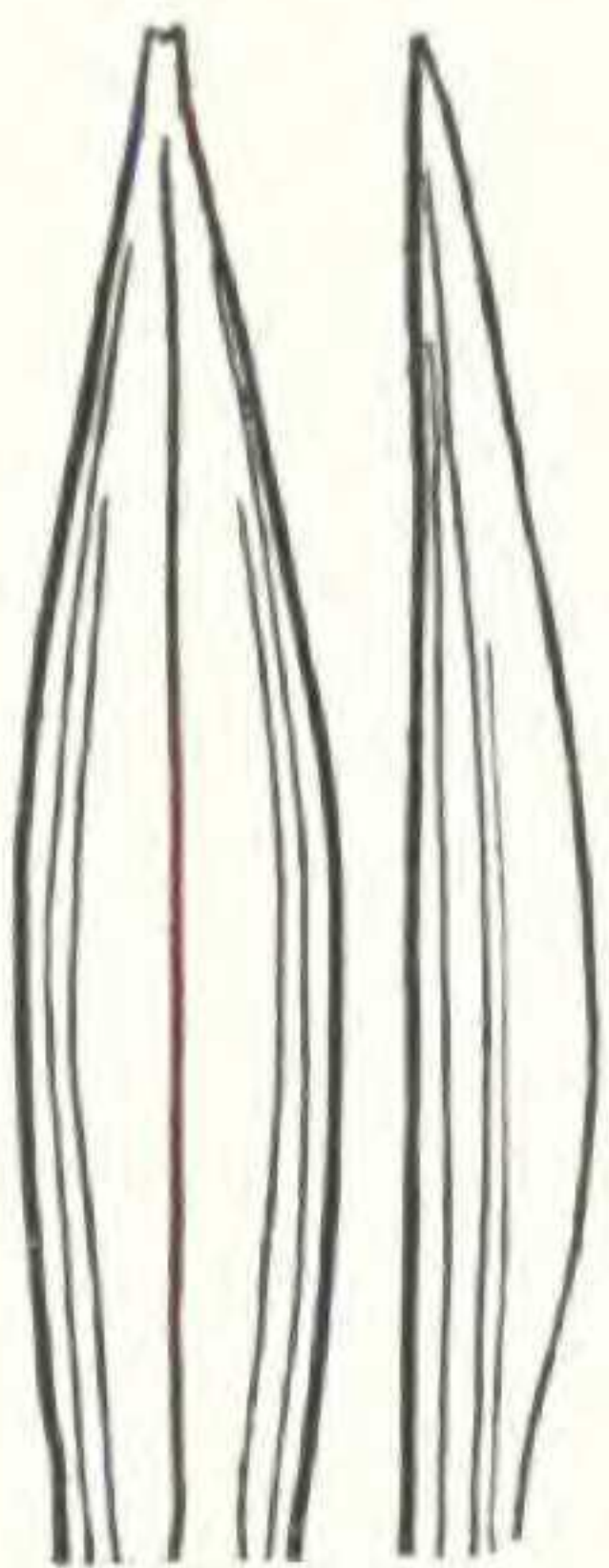
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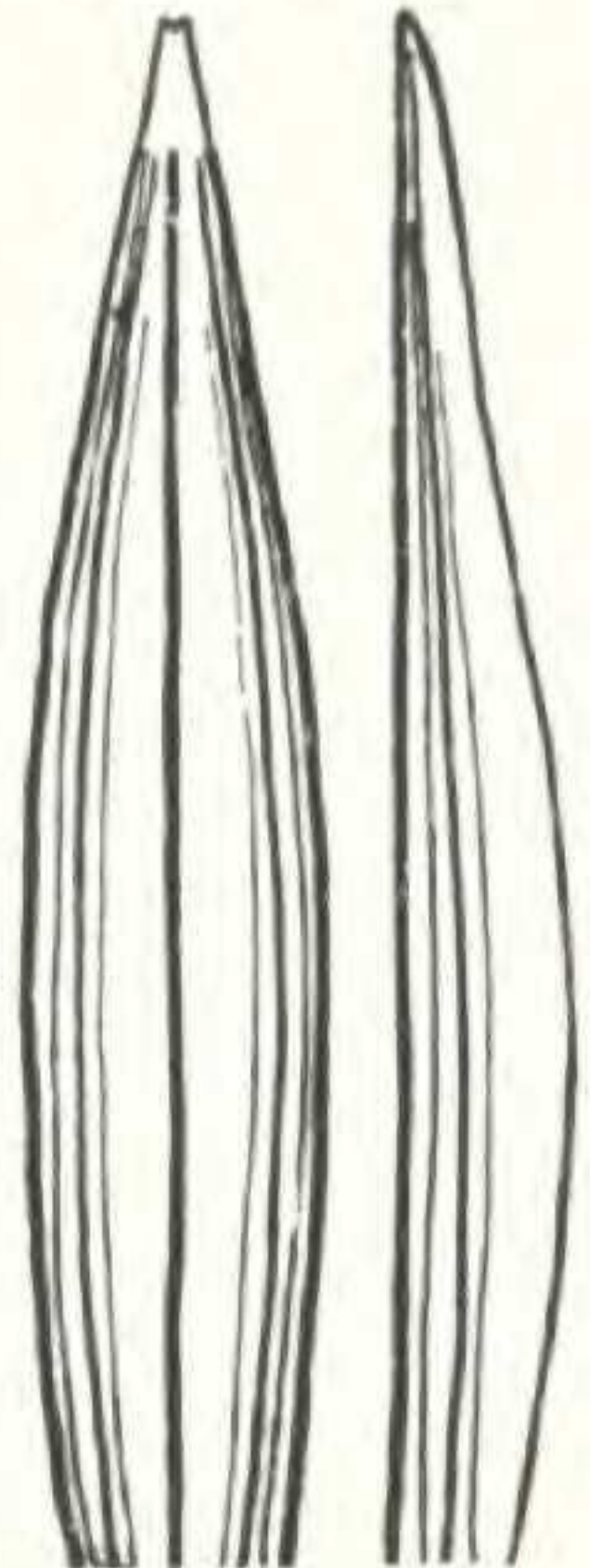
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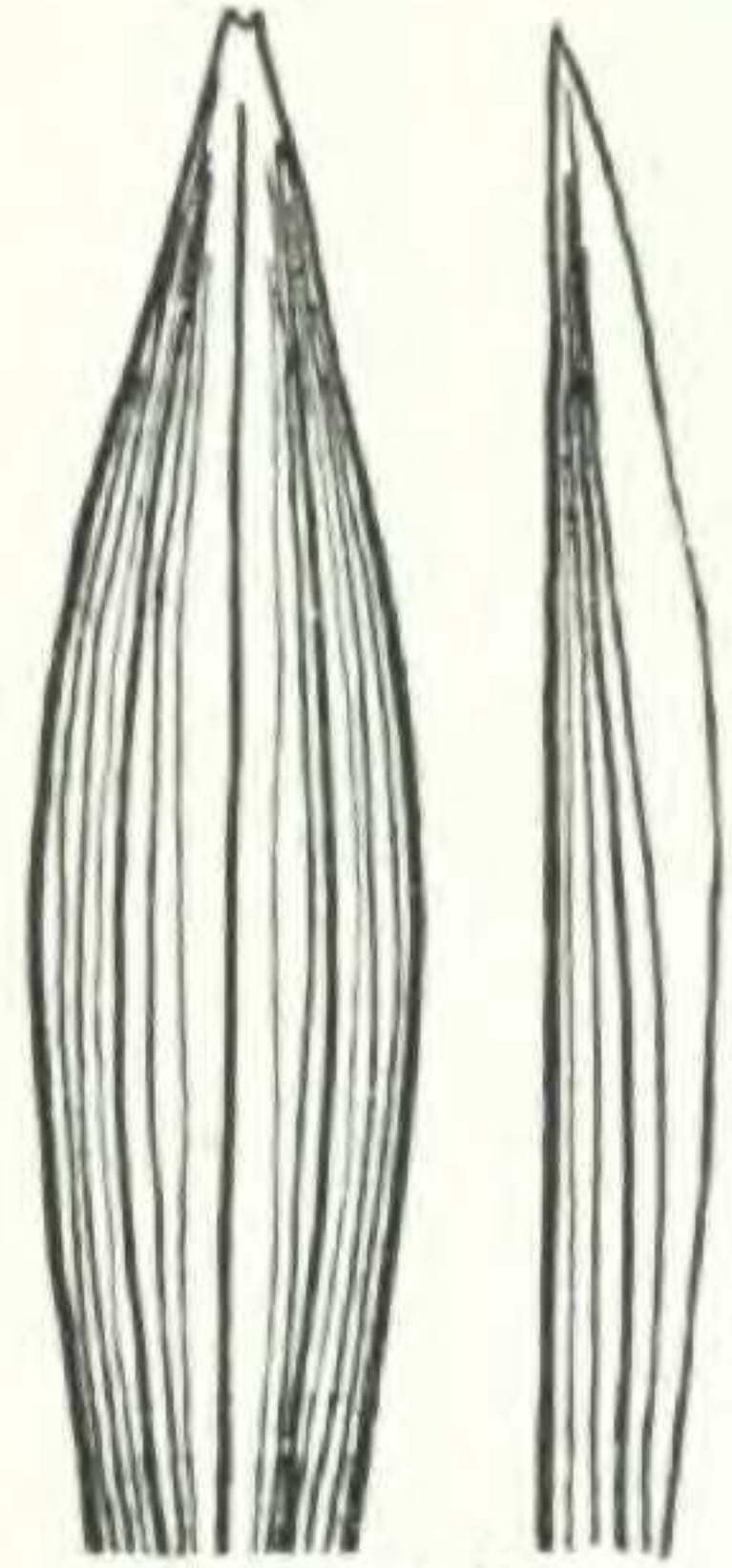
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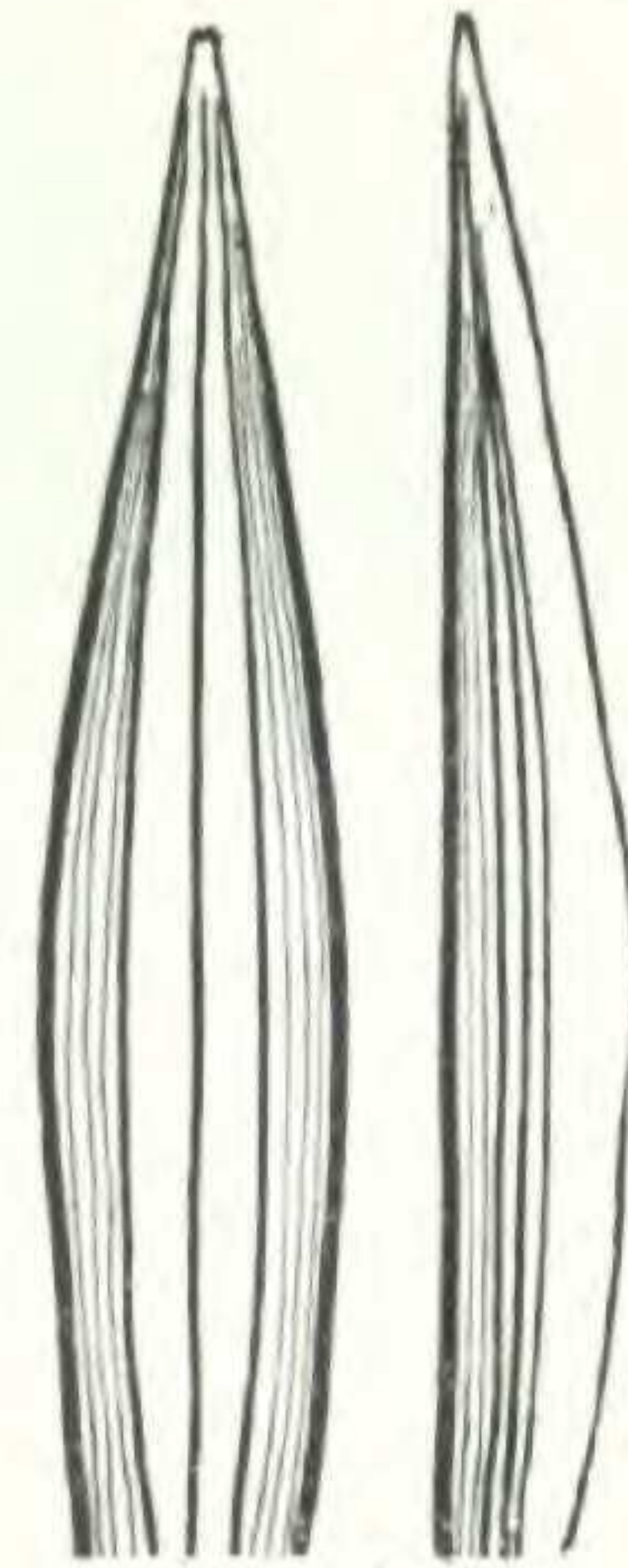
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112



113



114

THE MATERIAL FROM ARICA

The tassel specimen from the Quiani excavation, Division I, Layer D 1, is the most complete of all the tassels from Arica. It is rather small and in many respects simulates the tassels of certain present-day South American popcorn varieties. At its 7 nodes there are 17 secondary branches, of which the lowermost has again 2 tertiary branches. The longest complete secondary branches are 112–114 mm. in length (pl. 7, fig. 115). The central spike is nearly complete and measures 100 mm. long. Its uppermost and basal thirds are illustrated in figs. 116 and 117. The median third has not been illustrated because of its similarity to the uppermost third. The latter (fig. 116) has 8 nodes, with 3 spikelet pairs at 3 nodes and 2 spikelet pairs at 2 nodes. Of a total of 44 spikelets, 33 are sessile and 11 pedicellate. The lower portion (fig. 117) has 6 nodes at which the spikelet pairs are arranged as follows: 2 nodes with 3 pairs each, one node with 2 pairs, one node with 1 pair, one node with 2 pairs plus 1 spikelet, and one node with 1 pair plus 1 spikelet.

The first secondary branch (pl. 7, fig. 118), which is complete, is 114 mm. long. It has a very short sterile zone, if any. Of the 29 nodes, 27 have but one spikelet pair, and only the 2 nodes toward the tip of the branch have 2 spikelet pairs each. Of a total of 62 spikelets, 34 are sessile, the rest being either pedicellate or subsessile. The two tertiary branches (figs. 119 and 120), both of which have been broken, are attached at the base of the first secondary branch. One of them (fig. 119) contains 12 nodes, the other only 6 (fig. 120). In the shorter tertiary branch there are 4 nodes with one spikelet pair each, and 2 nodes with 4 spikelet pairs each. Of the total of 16 spikelets, 10 are sessile and 6 pedicellate. In the longer tertiary branch there is one spikelet pair at each node; of these 13 are pedicellate and 11 sessile.

Tassel No. 1 from Playa Miller Excavation, Level D 3 (pl. 8, fig. 128) has only 8 secondary branches and 3 tertiary branches at a total of 5 nodes. Since all the secondary and tertiary branches, as well as the central spike, are broken, it is not possible to tell their original lengths. As indicated in fig. 129, the upper half of the central spike has rather short internodes. At 18 of the nodes there is only one spikelet pair, at one of them 2 pairs, while at each of 4 nodes there are 3 spikelet pairs. Of the total of 66 spikelets, 52 are pedicellate, the rest sessile.

EXPLANATION OF PLATES 7 AND 8

Tassel and tassel-branch diagrams of the prehistoric material from Arica, Chile, collected by Mr. Junius Bird. The arrangement of the secondary and tertiary branches was studied by measuring the internodes in that part of the tassel. The lengths of the central spike and of the secondary and tertiary branches were measured. The lengths of the internodes of the central spike or of a part of it and of one or two more representative secondary and tertiary branches were measured as well as those of the spikelet pedicels. Finally, the number of spikelets per node was counted. The detailed diagrams were constructed to the scale 1:10 and later reduced one-fifth (twice natural size). In the drawings the solid ovals represent spikelets which were present on the specimen; the hollow ovals, spikelets which had been lost. If the pedicel were broken, this is indicated by two dots; if the pedicel were still complete, but only the spikelet lost, the missing spikelet is indicated by a hollow oval. Variation in glume length is not indicated.

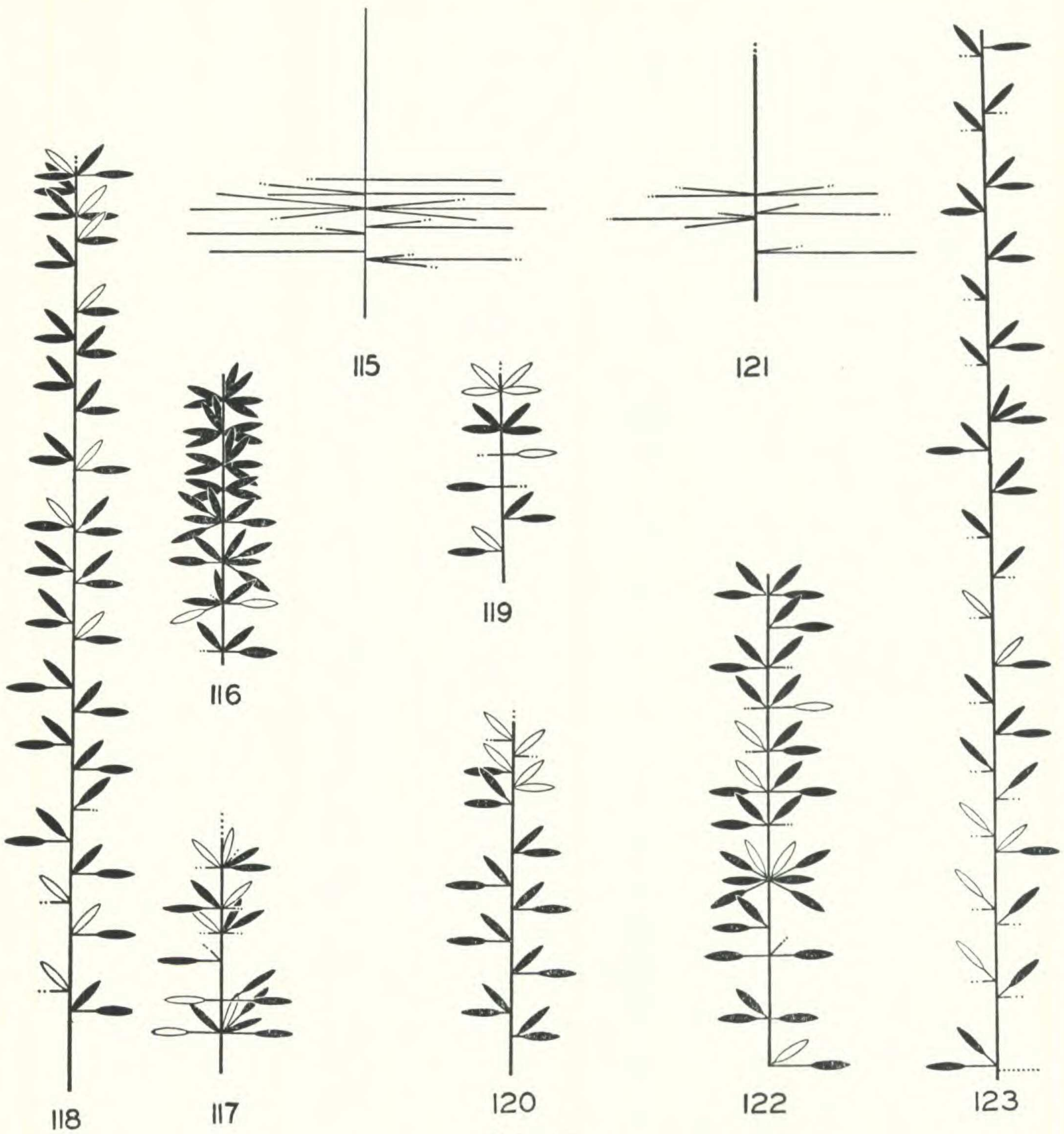
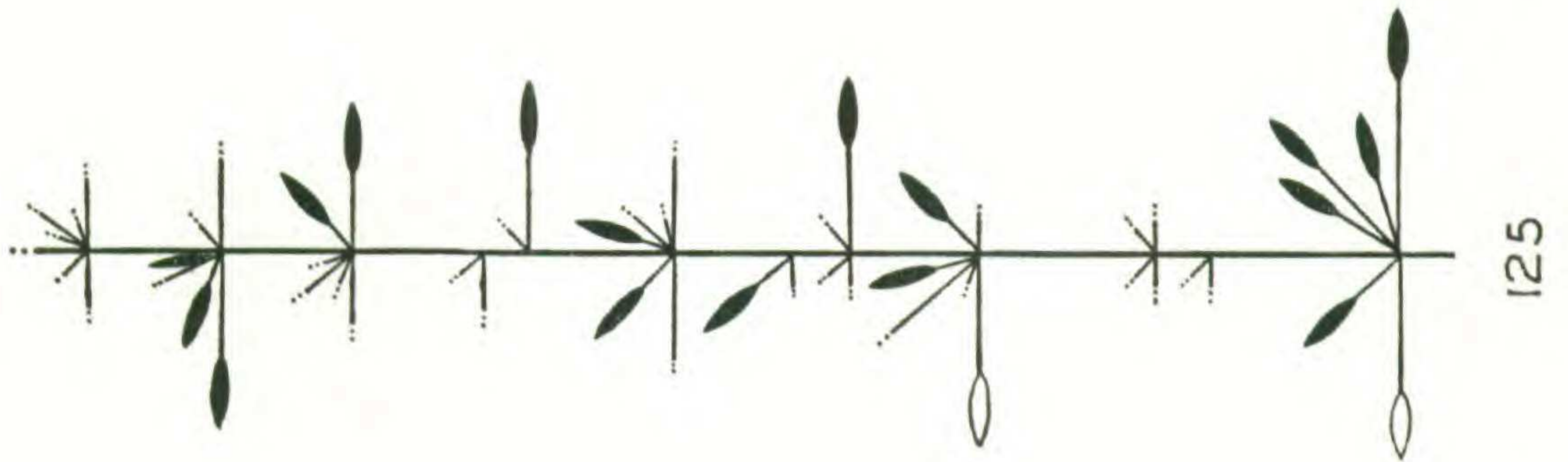
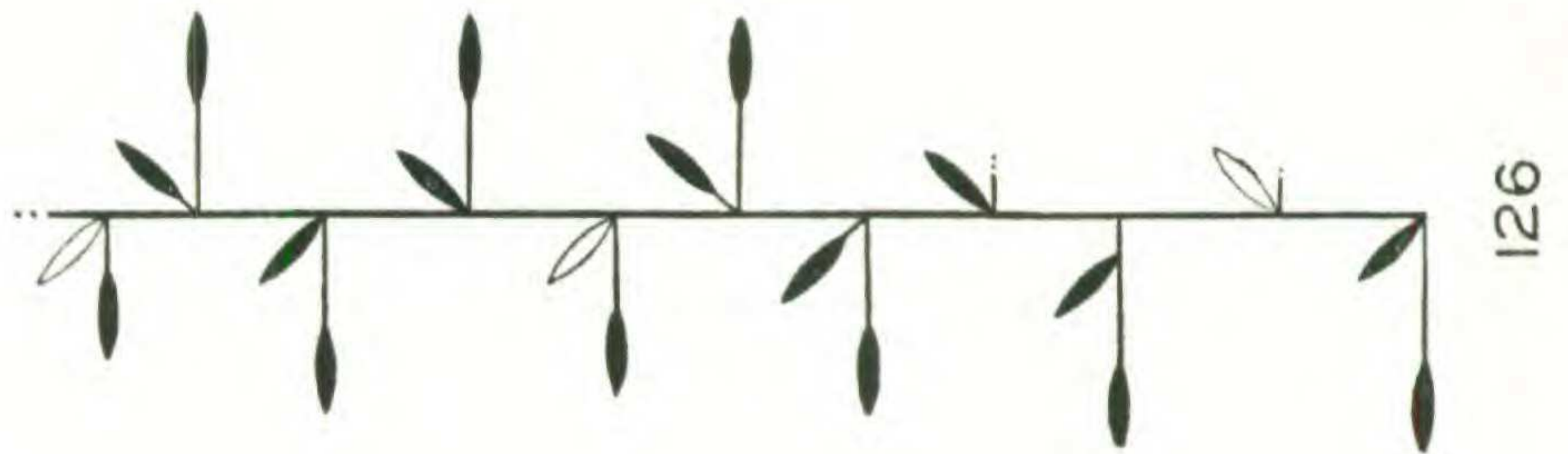
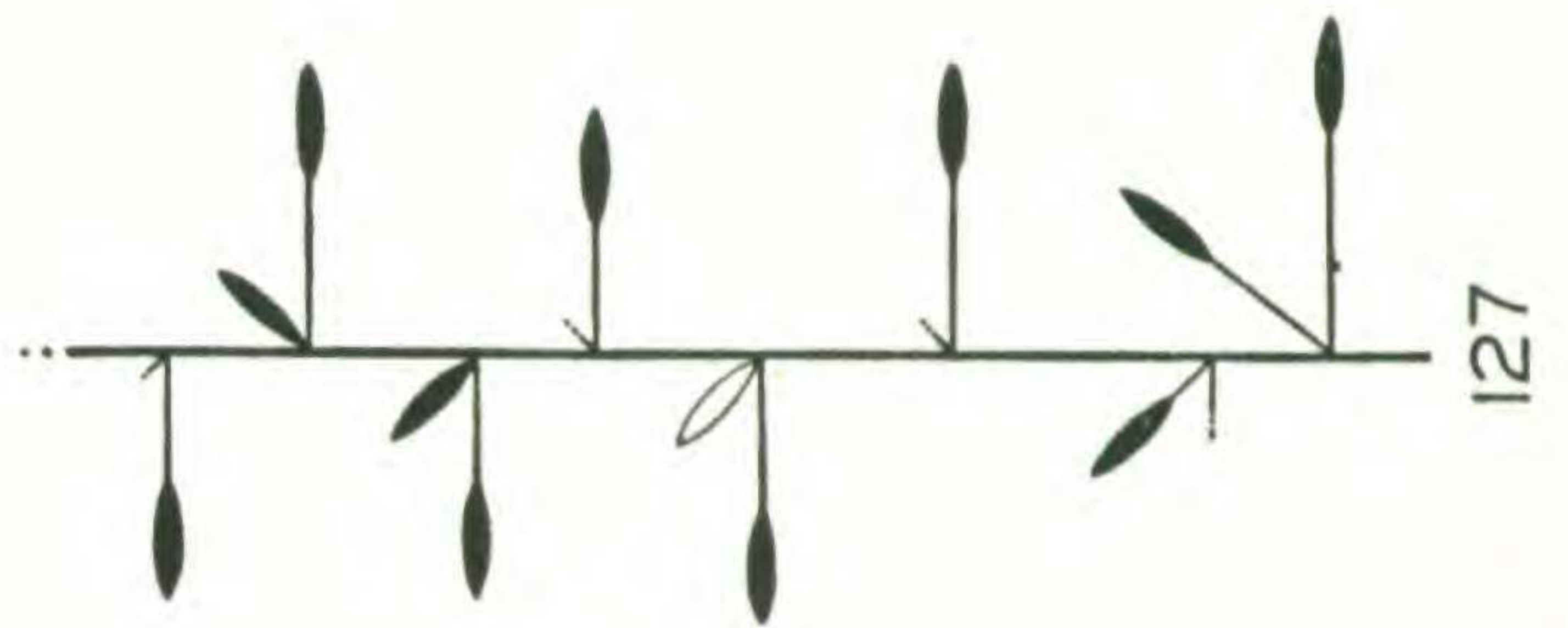
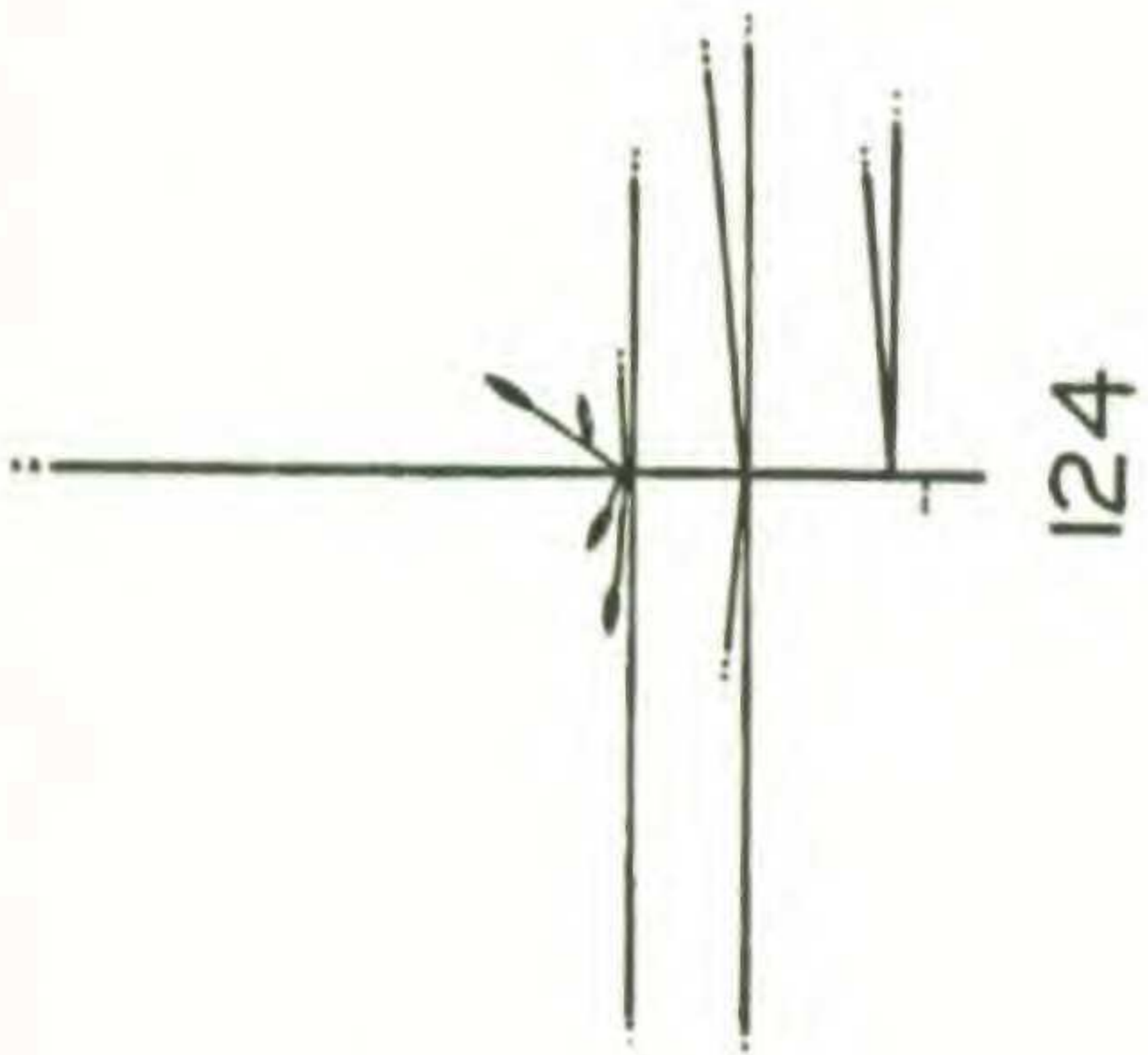
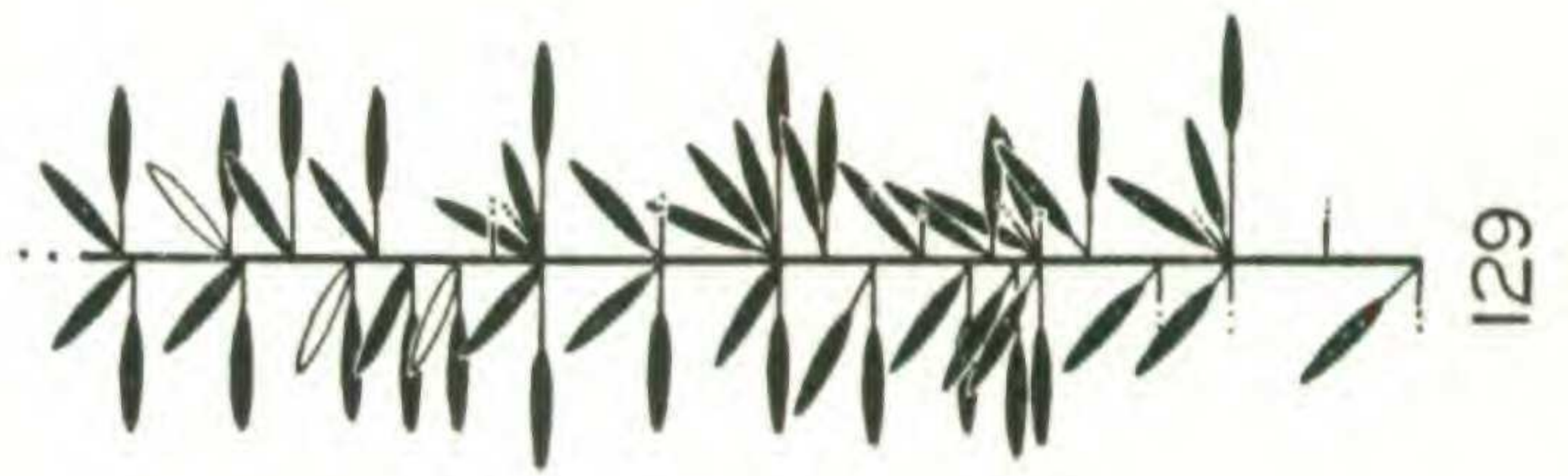
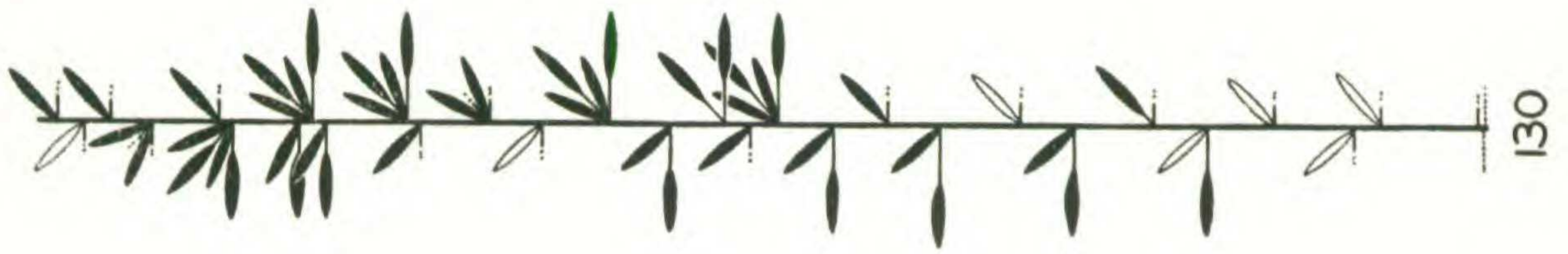


PLATE 7

Figs. 115-120. Quiani Excavation, Division I, Layer D 1:
 Fig. 115. The tassel.
 Fig. 116. Uppermost portion of the central spike.
 Fig. 117. Basal portion of the central spike.
 Fig. 118. Lowermost secondary branch.

Fig. 119. Tertiary branch.
 Fig. 120. Tertiary branch
 Figs. 121-123. Playa Miller Excavation, Level ABC:
 Fig. 121. The tassel.
 Fig. 122. Central spike.
 Fig. 123. Lowermost secondary branch.



The secondary branch (pl. 8, fig. 130) at the base of which the tertiary branches were attached has no sterile zone at the base. Of a total of 29 nodes, at 21 there is one spikelet pair, at one node one spikelet only, and at 7 nodes two spikelet pairs each, the result either of multiplication or of condensation. Of the total of 71 spikelets, 37 are pedicellate and 34 sessile.

Tassel No. 2 from Playa Miller Excavation, Level D 3, consists of 10 secondary branches at 4 nodes (pl. 8, fig. 124). All are broken, the longest branch being now only 9.5 cm. long. At the same node where the uppermost secondary branches are attached there are two spikelet pairs present as well. The broken central spike (fig. 125) has 12 nodes; at 6 of these there are 3 spikelet pairs each, at 2 there are 2 pairs each, and at the remaining 4 there is only one spikelet pair each. All the spikelets except one are pedicellate or subsessile.

The uppermost secondary branch has 11 nodes (pl. 8, fig. 126), at each of which there is only one spikelet pair. Of the spikelets, 14 are pedicellate or subsessile and 8 are sessile. In the lower secondary branch (fig. 127) at each of the 8 nodes there is 1 spikelet pair—13 pedicellate or subsessile spikelets and 3 sessile ones.

The tassel from Playa Miller Excavation, Level ABC (pl. 7, fig. 121) consists of 11 secondary branches at 4 nodes. All the branches, as well as the central spike, are broken except the lowermost secondary branch, which is 114 mm. long. The central spike (fig. 122) has 12 nodes; at one node 4 spikelet pairs, at 6 nodes 2 pairs, at 3 nodes only 1 pair, and at 2 nodes 1 pair plus one extra spikelet. The complete lowermost secondary branch (fig. 123) has 28 nodes; at 26 of them there is only one spikelet pair each, at 1 node only 1 spikelet, and at another node 1 pair plus 1 extra spikelet.

THE MATERIAL FROM BAT CAVE

In level IV at Bat Cave in New Mexico there were one more-or-less complete tassel and five tassel fragments. Despite the broken tips of the branches and of the central spike, tassel IV-329-3 (pl. 9) still shows that the branching was sparse; at 3 nodes there were only 4 secondary branches altogether; there are no tertiary branches and no sterile zones at the base of the secondary branches. On the central spike, 9 of the nodes are present, and the spikelets are arranged with one spikelet

EXPLANATION OF PLATE 8

- Figs. 124–127. Playa Miller Excavation, Level D 3, No. 2:
 Fig. 124. The tassel.
 Fig. 125. Central spike.
 Fig. 126. Uppermost secondary branch (that to the left in fig. 124).
 Fig. 127. Lowermost secondary branch.
 Figs. 128–130. Playa Miller Excavation, Level D 3, No. 1.
 Fig. 128. The tassel.
 Fig. 129. Uppermost half of the central spike.
 Fig. 130. Second lowest secondary branch.

pair at each of 4 nodes, 2 spikelet pairs at 1 node, only 1 spikelet at each of 2 nodes, and 1 spikelet pair and a single spikelet at 2 nodes. Of the total 20 spikelets, 2 are sessile and 18 pedicellate with rather long pedicels. Of the uppermost secondary branch there are only 2 nodes left, with 1 spikelet pair at each. The secondary branch to the left has 15 nodes, at 13 of which there is one spikelet pair each; at one node there is a spikelet pair plus a single spikelet, and at another there is only a single spikelet. The secondary branch to the right has 7 nodes, at 5 of which there is only one spikelet pair each and at 2 only a single spikelet each. Of the spikelets, 5 are sessile or subsessile and 7 are pedicellate. The fragmentary lowermost secondary branch has 9 nodes, at 8 of which there is 1 spikelet pair each and at 1 a single spikelet. There are in all 17 spikelets, 11 being pedicellate and 6 sessile or subsessile.

The fragment of a central spike from level IV (IV-329-1, pl. 9) has 4 nodes at each of which there are two spikelet pairs. All the spikelets are sessile. The fragment IV-329-2 is either from a lateral branch or from a central spike, more probably the latter. It has 14 nodes, at 6 of which there is one spikelet pair each, and at each of the remaining 8 nodes there are 2 spikelet pairs. Of the total of 44 spikelets, 23 are sessile and 21 pedicellate.

Fragment IV-301-1 (pl. 9) is from a lateral branch and has 16 nodes. At 5 of these there is one spikelet pair each; at 2 there are 2 pairs each; at 5 there are 1 spikelet pair and a single spikelet each; and at 4 only a single spikelet each. Of the 37 spikelets, 20 are sessile or subsessile and 17 are pedicellate. The central spike fragment IV-301-2 has only 4 nodes, at 2 of which there are 2 spikelet pairs and a single spikelet each, while at one node there is only one spikelet pair. At one of the nodes there are 6 spikelets altogether in 2 sets of 3 spikelets supported by a single pedicel.

From level V we have two fragments of tassels, one of a lateral branch and one of a central spike. The rather long fragment of the lateral branch (pl. 9, V-212), with 22 nodes, has a single spikelet pair at each node except for one at which there is only a single spikelet. At the basal portion of the fragment the spikelet pairs are arranged on one side of the main axis while in the upper portion they are arranged alternately at two sides of the main axis. Of the 43 spikelets 21 are sessile or subsessile and 22 pedicellate.

EXPLANATION OF PLATE 9

Tassel and tassel-fragment diagrams of the prehistoric material from Bat Cave, New Mexico, forwarded by Dr. Paul C. Mangelsdorf. The method of studying this material and making the drawings is the same as that used for making the detailed drawings of the central spikes and the tassel branches as indicated in "Explanation of Plates 7 and 8."

Fragment IV-301-1, from a lateral branch
 Fragment V-186, from a central spike.
 Fragment IV-329-2, from a lateral branch.
 Fragment IV-301-2, from a central spike.
 Fragment IV-280, from a lateral branch.

Fragment IV-329-1, from a central spike.
 Tassel IV-329-3.
 Fragment VI-128, from a lateral branch.
 Fragment V-212, from a lateral branch.

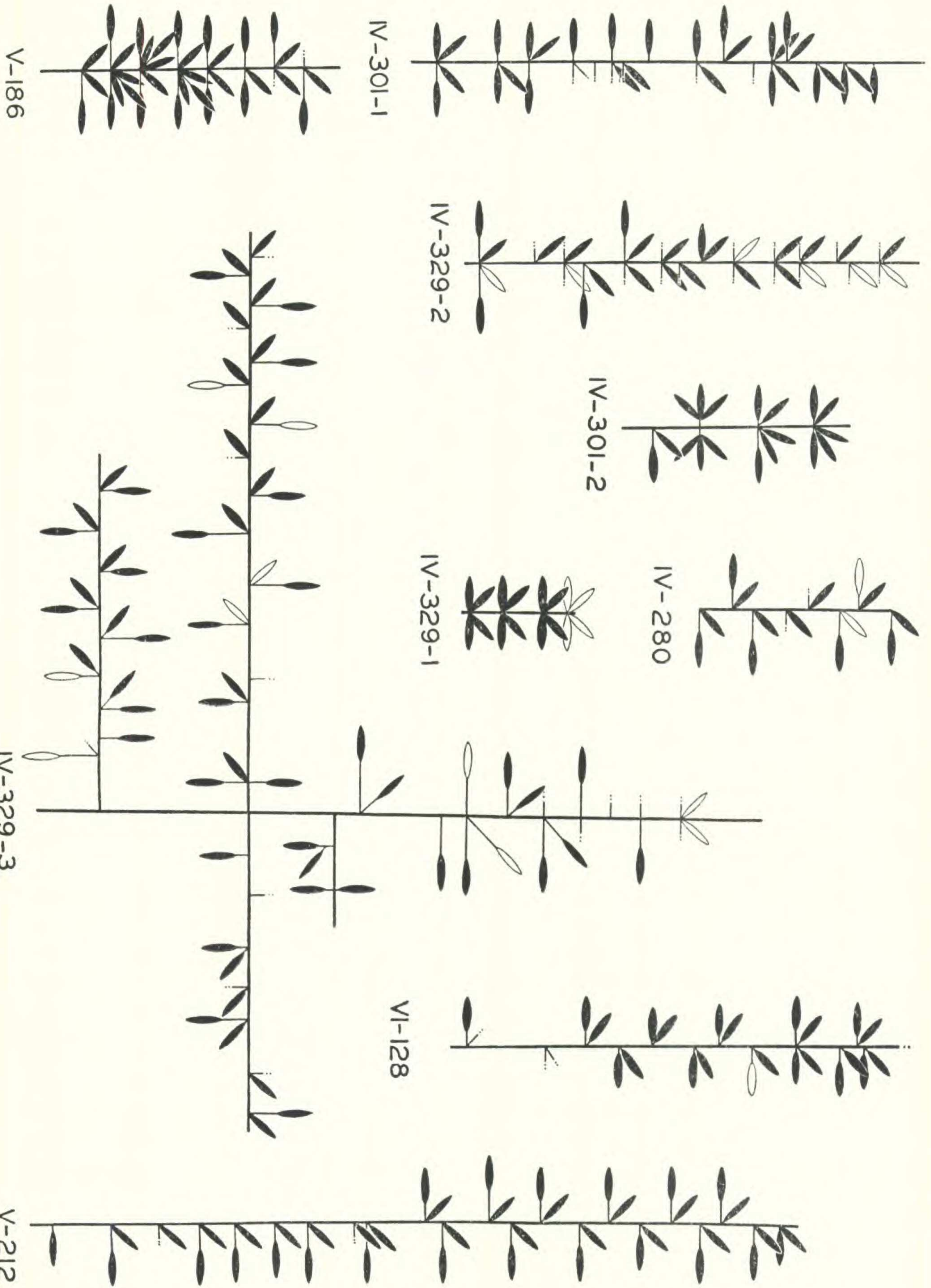


PLATE 9

The fragment of a central spike V-186 (pl. 9) has 8 nodes, with 3 spikelet pairs at each of 3 nodes, 2 pairs each at 2 nodes, and 1 pair and 1 single spikelet at each of 3 nodes. Of the 35 spikelets, 18 are sessile and 17 are pedicellate.

From the most recent stratum, Level VI, there is only one fragment, VI-128 (pl. 9), which is the distal end of a lateral branch. It has 12 nodes, at 11 of which there is one spikelet pair each, at the remaining one two spikelet pairs. Of the spikelets 16 are sessile or subsessile and 8 are pedicellate.

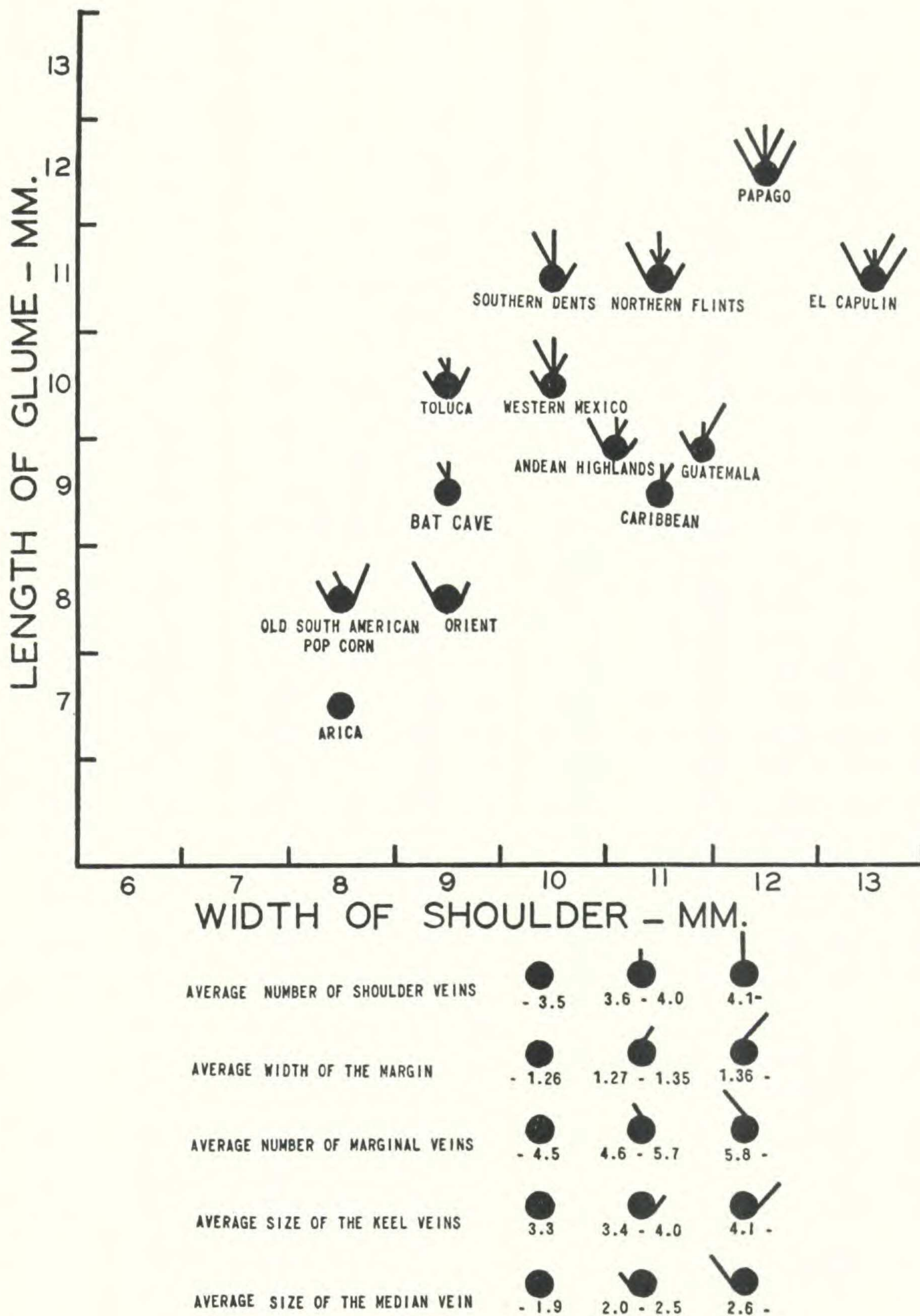
To the extent that any conclusions can be drawn from these few tassels and tassel fragments, the material from Bat Cave seems to be more variable than that from Arica. Of the four tassels from Arica the one we have called tassel No. 2 from Playa Miller Excavation, Level D 3, differs more from any one of the remaining three than these do from each other. It is characterized by long internodes and very long pedicels while the internodes and pedicels of the other three tassels are relatively short, giving the spikes a much denser aspect. Part of this effect may be the result of multiplication.

In the relatively scant material from Bat Cave no such coherent group of tassels can be singled out. The variability among the fragments is as great as that of several different varieties of modern maize. In several fragments there is some suggestion of the condensation which is so common in present-day North American varieties of maize.

DISCUSSION

Maize is a notoriously variable plant. These studies of variation in the male spikelet show that the staminate reproductive organ is no exception to the rule. Not only is there great variation between different varieties and races but also there is striking variation between the spikelets of a single tassel. Spikelet variation is therefore a valuable character, and a study of it seems to give as useful information about the varieties as does any other character. However, studying it is extremely time-consuming. A considerable number of measurements is required since the possible variation within the plant always has to be taken into consideration. Only averages can be used if one is to study variation between plants of a variety or variation between different varieties.

The most important results found here are presented as diagrams, since these give a clear picture of the variation of the material used. In reviewing them certain relationships are suggested which might serve as clues to classification in certain groups. However, until we know more about the interrelationships of the characters depicted here and others previously studied or as yet unanalyzed we cannot say with complete confidence that the suggested clues should form the basis of a final classification. Nevertheless, the results of these spikelet studies seem to correlate with those of previous studies which used different methods and different characters. One of the least variable groups studied is the collection of prehistoric tassels from Arica, Chile. The amount of material is not very large,



Text-fig. 4. Pictorialized scatter diagram showing relationships between variation in 7 different spikelet characters for various groups of maize. (For detailed explanation see p. 90). Each dot represents the mean for 7 measured characters for all the varieties studied in that group; horizontal axis, width of average glume shoulder; vertical axis, length of average glume; five other characters are diagrammed by rays, as explained above.

but it shows at least that three of these four tassel specimens have very similar spikelet characters (figs. 1-3, 115-118, 121-123, and 128-129, pls. 2, 7, and 8). The remaining one of the four tassels varies somewhat from these both in glume and in other spikelet characters (fig. 4 of pl. 2 and figs. 124-127, pl. 8). Among the modern varieties the material from Soledad, Cuba (figs. 23-26, pl. 2), Quito, Ecuador (figs. 35-38, pl. 3), Titicaca, Bolivia (figs. 31-33, pl. 3), and El Capulin, Mexico (figs. 96-105, pl. 6) form similar more or less uniform groups.

The other prehistoric collection, that from Bat Cave, New Mexico, is, on the contrary, extremely variable (pl. 2, figs. 5-11, and pl. 9). Modern Papago maize from Arizona, from the same general area as this prehistoric Basketmaker maize from Bat Cave, is also extremely variable (figs. 106-114, pl. 6). Not only is this variation great between the plants from different fields and different villages (figs. 111-114), but, as shown in figs. 106-110, it is also extremely great within one plant. In this respect it is quite different from the Mexican variety El Capulin (figs. 96-105, pl. 6), which has been taken as a typical example of a uniform variety. In El Capulin both the variation within the plant and the variation between plants from the same field are only slight.

If we take the material of this study as a whole, one of the general effects of the domestication of maize seems to have been an increase in size of the male glume. Apparently, in selecting for larger and larger kernels, man has unconsciously selected for factors which increase the sizes of all the floral parts. However, the increase in spikelet size with increased kernel size is far from being strictly proportional in all kinds of maize. This is strikingly demonstrated by the three kinds of maize, Argentine Pop, Cuzco Flour Corn, and Papago. Of these three, Argentine Pop has both the smallest kernels and the smallest glumes, while Cuzco, with by far the largest kernels, has glumes which are smaller than those of Papago. Ratios of increase in kernel size were found by weighing five kernels of each kind. Corresponding ratios for the glumes were calculated by taking the cube of glume length as a rough measure of volume. The two sets of ratios are as follows:

| | Argentine Pop | Cuzco | Papago |
|--------|---------------|-------|--------|
| Glume | 1 | 2.2 | 4.9 |
| Kernel | 1 | 25.0 | 4.0 |

One sees that the increase in kernel size in Papago maize is accompanied by a roughly proportional increase in glume size, while in the big Cuzco flour corn there has been a great increase in kernel size and only a slight increase in glume size.

EXPLANATION OF PLATE 10

Twelve pictorialized diagrams showing the variation and relationships of 7 measured spikelet characters within each major group of the varieties studied. Each dot represents the average values for one tassel. Horizontal and vertical axes and 5 additional characters scored as in text-fig. 4. On one diagram two similar varieties of Mexican pointed popcorn have been distinguished by solid and open dots.

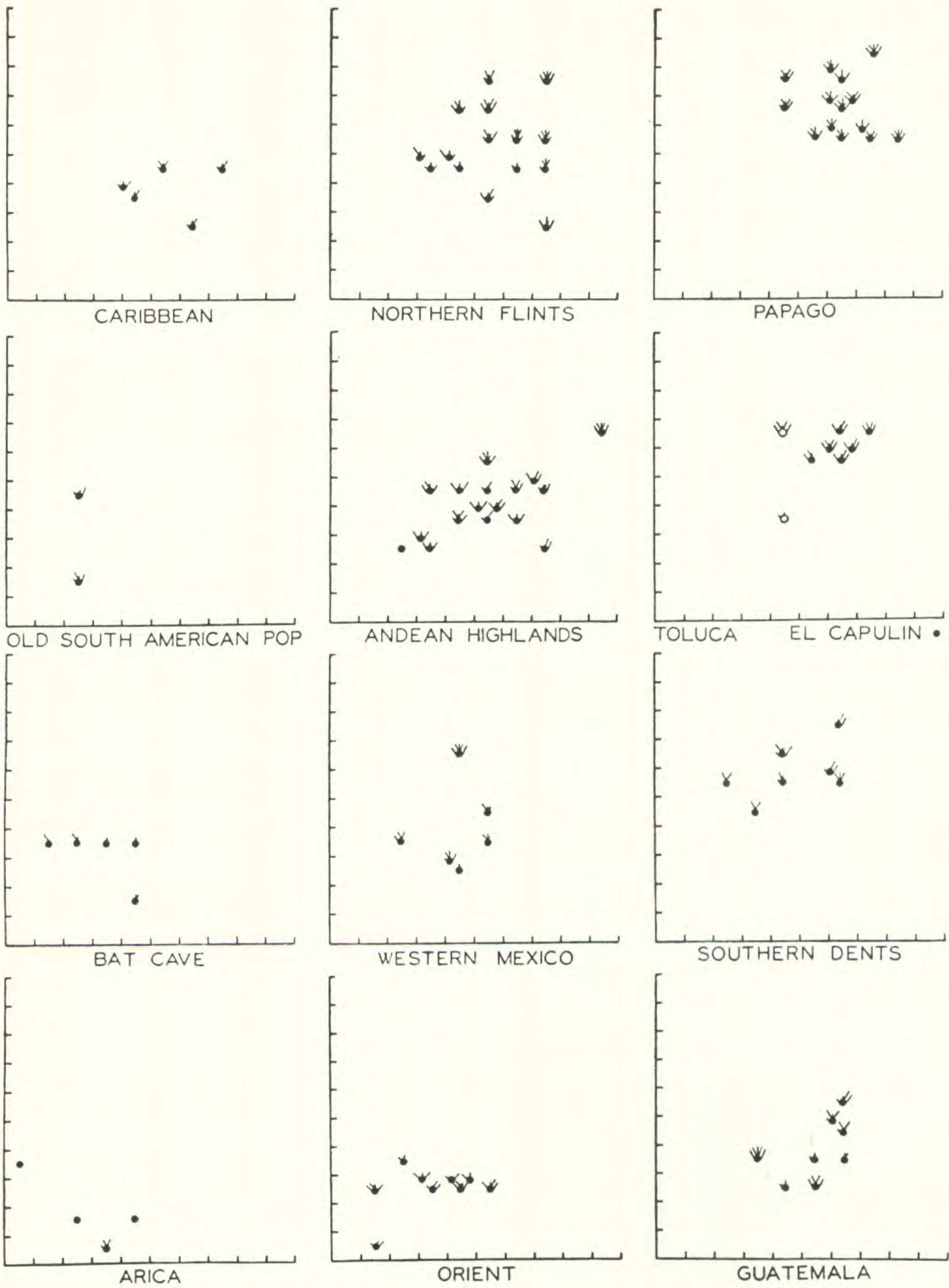


PLATE 10

The variation of seven characters between different groups of varieties is represented in text-fig. 4. With respect to the groups labelled "Orient" and "Old South American Pop Corn" we note that of their total of 14 characters 9 lie within the range of variation for the corresponding characters of the material from Arica and from Bat Cave. Similar analyses of the North American (including Mexican) groups of varieties shows that in all but one character (with three minor exceptions) the variation from the range for the Arica and Bat Cave material is in the same direction. We may summarize these statements by saying that with regard to the seven characters in question: (1) the material from the Orient and the old South American popcorn varieties are markedly intermediate between the varieties from Arica and those from Bat Cave, and (2) the North American material is not only not intermediate between these two varieties but the variation is almost completely in the other direction.

SUMMARY

An intensive study of variation in the male spikelet of maize was made for the following reasons: (1) Agronomists and ethnobotanists have ignored the male spikelet almost completely because it is of little economic importance. (2) However, for this very reason it has been only indirectly modified by human selection. (3) Experience with wild grasses related to maize points to the male spikelet as one of the most significant features for determining relationships of maize to its possible wild ancestors.

Methods of selecting spikelets for study, for scoring their variation exactly, and for making averages are described in detail. Semi-graphical methods were found most effective in presenting and analyzing the results.

The variation of spikelet and inflorescence characters in prehistoric tassels collected at Arica, Chile, and at Bat Cave, New Mexico, is described in detail. Variation in spikelet morphology was surveyed in the collections of modern maize at the Missouri Botanical Garden.

The following three generalizations can be made:

A. Different strains of maize have characteristically different degrees of variability. The maize of the Papago Indians is morphologically similar to that of the prehistoric Basketmakers and is the most variable in spikelet morphology of any variety in the collection. This extreme variability of Papago maize is shown in variation between different spikelets on the same plant, between averages for different plants from the same field, and between averages of different collections.

B. Central and North American varieties have more and heavier veins, narrower margins, longer and narrower tips, and stronger keels than prehistoric, oriental, and South American varieties. All these differences are in the direction to be expected from the hypothesis of Mangelsdorf and Reeves (1939) that North and Central American varieties have been extensively modified by introgression from *Tripsacum*.

C. Of the prehistoric material that from Arica, Chile, is much more uniform than the greatly variable material from Bat Cave, New Mexico, both in glume characters and in spikelet arrangement. Multiplication is apparently present in the material from Arica and condensation in the material from Bat Cave.

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APPENDIX I

List of varieties, their origin, and the groups to which they belong. If the varieties were grown outside their natural range, the place is given in parentheses. Explanation of group designations given on p. 77.

1. *Argentine Popcorn*: coll. Parodi, Argentina. (Johnston, Iowa). Group B 1.
2. *Arica*: Arica, Chile. (From the collection of Am. Mus. Nat. Hist.). Group A 1.
3. *Assam*: Naga Hill Tribes, Assam, India. (Gray Summit, Mo.). Group F.
4. *Bat Cave*: Bat Cave, Catron County, New Mexico. (From the collection of Bot. Mus. Harvard Univ.). Group A 2.
5. *Bolivia*, Mangelsdorf's #127895: Bolivia. (Cienfuegos, Cuba). Group B 2.
6. *Burmese Corn*: coll. E. Skarstrom, Telagua, Burma. Group F.
7. *Cherokee Indian Corn*: Cherokee Reservation, North Carolina. (Johnston, Iowa). Group E 1.
8. *China*, #149114 A and #149118: Chengtu, Szechuan, China. (Johnston, Iowa). Group F.
9. *Chinese Waxy*: Shanghai (?), China. (Blandy Exp. Farm, Va.). Group F.
10. *Chiripó Indian Corn*: Costa Rica. (Johnston, Iowa). Group C 3.
11. *Chukut Kuk*: Papago Indian Reservation, Arizona. Group E 2.
12. *Coroico*: Coroico, Alcocha, Bolivia. Group B 2.
13. *Cold Fields*: Papago Indian Reservation, Arizona. Group E 2.
14. *Coyote*: Papago Indian Reservation, Arizona. Group E 2.
15. *Creole Flint*: Southern United States. (Johnston, Iowa). Group D 2.
16. *Culiacán*: Culiacán, Sinaloa, Mexico. (Gray Summit, Mo.). Group C 1.
17. *Cuzco*: Arubamba, Cuzco, Peru. (Arcadia, Cal.). Group B 2.
18. *14-row Dakota Flint*: South Dakota. (Johnston, Iowa). Group E 1.
19. *Dryden*: Northeastern United States. (Johnston, Iowa). Group E 1.
20. *Early Quebec Flint*: Restigouche, Que., Canada. (Johnston, Iowa). Group E 1.
21. *Elberta*: Baldwin Co., Alabama. (Johnston, Iowa). Group E 3.
22. *El Capulín*: El Capulín, Mexico. Group C 2.
23. *Fort Kent*: Northern Maine, United States. (Johnston, Iowa). Group E 1.
24. *Hackberry*: Ozark Mountains, United States. (Arcadia, Cal.). Group E 3.
25. *Harris Mammoth Yellow*: Old United States variety. (Johnston, Iowa). Group E 1.
26. *Hickory King*: Old United States variety. (Ames, Iowa). Group E 3.
27. *India*: India. (Gray Summit, Mo.). Group F.
28. *Kerwo*: Papago Indian Reservation, Arizona. Group E 2.
29. *Knighton Little Cob Flint*: Old United States variety. (Blandy Exp. Farm, Va.). Group E 3.
30. *Latham's Double*: Old United States variety. (Blandy Exp. Farm, Va.). Group E.
31. *Longfellow*: Old United States variety. (Johnston, Iowa). Group E 1.
32. *Louisiana Gourseed*: Texas, United States. (Gray Summit, Mo.). Group E 3.
35. *Maíz chapolote*: Culiacán, Sinaloa, Mexico. (Gray Summit, Mo.). Group C 1.
36. *Maíz de elote*: coll. Isabel Kelly, Western Mexico. (Arcadia, Cal.). Group C 1.
37. *Maíz reventador*: Coalcomán, Michoacán, Mexico. (Johnston, Iowa). Group C 1.
38. *Maíz reventador*: coll. Isabel Kelly, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
33. *Mandan Yellow Flour*: Northern Great Plains, United States. (Johnston, Iowa). Group E 1.
34. *Manglaralto*: Manglaralto, Ecuador. Group B 2.
39. *Papago*: Lochiel, Arizona. (Johnston, Iowa). Group E 2.
40. *Parker's Flint*: Potsdam, N. Y. (Johnston, Iowa). Group E 1.
41. *Pia Oik*: Papago Indian Reservation, Arizona. Group E 2.
42. *Quito*: Pomasqui, Quito, Ecuador. (Arcadia, Cal.). Group B 2.
43. *Río Loa*: Chiu-Chiu, Chile. (Arcadia, Cal.). Group C 1.
44. *Sa 15 b-4*: Maíz reventador, Jalisco, Mexico. (Blandy Exp. Farm, Va.). Group C 1.
45. *San Andreas*, Cutler's #109: San Andreas Villa Sur, Guatemala. Group C 3.
46. *Santa Lucia*: Santa Lucia, Guatemala. Group C 3.
47. *Sauer's #11-4*: Maíz reventador, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
48. *Siamese Popcorn*: Bangkok, Siam. (La Jolla, Cal.). Group F.
49. *Soledad*: Soledad, Cuba. Group D 1.
50. *Stevens Flint*: Ithaca, N. Y. (Johnston, Iowa). Group E 1.
51. *Talpa*: Talpa, Jalisco, Mexico. (Arcadia, Cal.). Group C 1.
52. *Tama Flour Corn*: Tama Indians, Iowa. (Johnston, Iowa). Group E 1.
53. *Tennessee Red Cob*: Old United States variety. (Blandy Exp. Farm, Va.). Group E 3.
54. *Titicaca*: Titicaca, Bolivia. Group B 2.
55. *Toluca*: Toluca, Mexico. (Gray Summit, Mo.). Group C 2.
56. *Topawa*: Papago Reservation, Arizona. Group E 2.
57. *Turkish Popcorn*: Anatolia, Turkey. (Ames, Iowa). Group F.
58. *Valle*: Sucre, Bolivia. Group B 2.

APPENDIX II

TABLE OF AVERAGES OF MEASUREMENTS FOR TEN CHARACTERS IN TWENTY
GLUMES OF EACH VARIETY

| Name of variety | Figure number | Average length of glume (mm.) | Average length of median vein (mm.) | Average width of right margin (mm.) | Average width of right shoulder (mm.) | Average number of marginal veins | Average number of shoulder veins | Average size of keel vein* | Average size of median vein* | Average size of right marginal veins* | Average size of right shoulder veins* |
|--|---------------|-------------------------------|-------------------------------------|-------------------------------------|---------------------------------------|----------------------------------|----------------------------------|----------------------------|------------------------------|---------------------------------------|---------------------------------------|
| Argentine Popcorn | 21 | 7.09 | 6.91 | 1.12 | 0.82 | 3 | 2 | 4 | 2 | 1,2,1 | 1,1 |
| Arica, Quiani Exc. Div. I, D1 | 1 | 6.72 | 6.36 | 1.36 | 0.98 | 3 | 2 | 3 | 2 | 0,1,1 | 0,1 |
| Arica, Playa Miller Exc. Layer ABC | 2 | 7.11 | 5.51 | 0.99 | 0.88 | 2 | 2 | 3 | 1 | 0,1 | 1,0 |
| Arica, Playa Miller Exc. Layer D3, #1 | 3 | 7.56 | 6.53 | 1.07 | 1.00 | 2 | 1 | 3 | 1 | 0,1 | 0 |
| Arica, Playa Miller Exc. Layer D3, #2 | 4 | 9.48 | 8.00 | 1.08 | 0.65 | 2 | 1 | 3 | 1 | 0,1 | 0 |
| Assam #1074 | 16 | 8.66 | 6.87 | 0.99 | 0.97 | 1 | 2 | 4 | 3 | 1 | 1,2 |
| Assam #44 | 17 | 8.85 | 7.94 | 1.18 | 1.07 | 1 | 2 | 3 | 3 | 2 | 2,2 |
| Bat Cave VI-128 | 5 | 7.50 | 4.75 | 1.32 | 1.00 | 2 | 2 | 1 | 0 | 0,1 | 1,0 |
| Bat Cave V-186 | 9 | 8.50 | 8.25 | 1.17 | 1.17 | 3 | 2 | 1 | 1 | 0,0,0 | 0,0 |
| Bat Cave IV-280 | 7 | 9.25 | 8.80 | 1.00 | 0.98 | 2 | 2 | 1 | 1 | 0,1 | 0,0 |
| Bat Cave IV-301-2 | 11 | 12.20 | 11.70 | 1.30 | 1.15 | 4 | 3 | 4 | 2 | 0,2,0,0 | 0,0,0 |
| Bat Cave IV-329-1 | 6 | 9.20 | 8.15 | 1.12 | 0.80 | 4 | 2 | 1 | 0 | 0,1,0,0 | 0,0 |
| Bat Cave IV-329-2 | 8 | 9.90 | 9.00 | 1.02 | 1.02 | 3 | 2 | 2 | 1 | 0,1,0 | 0,0 |
| Bat Cave IV-329-3 | 10 | 9.60 | 8.20 | 1.20 | 0.72 | 3 | 1 | 1 | 1 | 0,1,0 | 0 |
| Bolivia, Mangelsdorf's #127895 | 28 | 8.44 | 6.50 | 1.13 | 0.95 | 2 | 2 | 4 | 4 | 1,2 | 3,2 |
| Burmese Corn | 13 | 8.37 | 7.67 | 1.28 | 1.00 | 3 | 2 | 5 | 3 | 2,3,2 | 2,2 |
| Cherokee Indian Corn #1 | 72 | 8.77 | 7.00 | 1.32 | 1.32 | 2 | 2 | 4 | 2 | 1,2 | 1,1 |
| Cherokee Indian Corn #2 | 73 | 10.15 | 5.59 | 1.25 | 1.22 | 3 | 2 | 5 | 3 | 2,2,2 | 2,3 |
| China #149114A | 19 | 8.30 | 6.00 | 1.52 | 0.92 | 1 | 1 | 4 | 2 | 2 | 2 |
| China #149118 | 20 | 6.82 | 5.87 | 1.27 | 0.75 | 2 | 1 | 4 | 2 | 1,2 | 1 |
| Chinese Waxy | 18 | 8.90 | 7.65 | 1.17 | 1.00 | 2 | 1 | 4 | 2 | 2 | 2,2 |
| Chiripo Indian Corn | 84 | 8.37 | 7.77 | 1.47 | 1.12 | 3 | 2 | 5 | 3 | 3,3,3 | 3,3 |
| Chukut Kuk #1 | 111 | 12.84 | 11.70 | 1.46 | 1.29 | 3 | 2 | 4 | 3 | 2,2,1 | 2,2 |
| Chukut Kuk #2 | 112 | 13.22 | 12.06 | 1.92 | 1.81 | 3 | 3 | 4 | 4 | 2,3,1 | 1,3,2 |
| Chukut Kuk #3 | 113 | 12.55 | 11.86 | 1.38 | 1.46 | 4 | 6 | 4 | 3 | 1,2,3,2 | 1,2,3, 1,2,2 |
| Chukut Kuk #4 | 114 | 14.39 | 13.85 | 1.58 | 1.36 | 5 | 4 | 5 | 3 | 1,1,3, 3,2 | 3,1,1, 1 |
| Coroico #6094-2 | 29 | 9.22 | 7.87 | 1.68 | 1.17 | 2 | 1 | 3 | 2 | 2,2 | 2 |
| Cold Fields #5 | 93 | 13.80 | 13.14 | 1.29 | 1.28 | 2 | 3 | 5 | 3 | 2,3 | 1,2,2 |
| Coyote #1 | 86 | 11.73 | 10.90 | 1.52 | 1.28 | 3 | 3 | 3 | 2 | 1,1,1 | 1,1,1 |
| Coyote #2 | 92 | 13.90 | 13.49 | 1.53 | 1.04 | 3 | 2 | 4 | 2 | 1,1,1 | 1,1 |
| Creole Flint | 27 | 9.63 | 9.57 | 1.14 | 1.04 | 2 | 2 | 5 | 2 | 2,2 | 2,2 |
| Culiacán #1-8 | 49 | 10.06 | 9.14 | 1.35 | 1.18 | 3 | 2 | 3 | 1 | 1,1 | 1,2,1 |
| Cuzco #10-2 | 40 | 9.31 | 8.72 | 1.18 | 1.20 | 1 | 2 | 4 | 3 | 2 | 2,2 |
| Cuzco #9-2 | 41 | 9.32 | 8.56 | 1.37 | 1.19 | 2 | 2 | 5 | 4 | 3,4 | 3,3 |
| Cuzco #8-9 | 42 | 9.78 | 8.55 | 1.60 | 1.01 | 3 | 2 | 4 | 2 | 2,2,2 | 2,2 |
| Cuzco #4-3 | 43 | 10.26 | 8.39 | 1.38 | 1.10 | 2 | 1 | 3 | 2 | 2,2 | 2 |
| Cuzco #3-1 | 44 | 12.30 | 10.88 | 1.70 | 1.52 | 4 | 4 | 5 | 4 | 2,3,3, 2 | 2,2,2, 2 |
| 14-row Dakota Flint | 66 | 11.81 | 10.85 | 1.31 | 1.16 | 3 | 2 | 4 | 2 | 2,2 | 2,3,1 |
| Dryden | 62 | 11.12 | 9.69 | 1.46 | 1.28 | 3 | 3 | 4 | 2 | 2,3,2 | 2,2,2 |

*Scored as in fig. 3.

APPENDIX II (Continued)

| Name of variety | Figure number | Average length of glume (mm.) | Average length of median vein (mm.) | Average width of right margin (mm.) | Average width of right shoulder (mm.) | Average number of marginal veins | Average number of shoulder veins | Average size of keel vein* | Average size of median vein* | marginal veins* marginal veins* | Average size of right shoulder veins* |
|---------------------------------|---------------|-------------------------------|-------------------------------------|-------------------------------------|---------------------------------------|----------------------------------|----------------------------------|----------------------------|------------------------------|------------------------------------|---------------------------------------|
| Early Quebec Flint | 63 | 10.61 | 9.68 | 0.86 | 1.01 | 1 | 2 | 3 | 3 | 2,1 | 2 |
| Elberta | 53 | 11.38 | 11.29 | 1.42 | 0.80 | 3 | 1 | 3 | 1 | 1 | 1,2,1 |
| El Capulín #1059 | 102 | 11.93 | 10.83 | 1.59 | 1.36 | 2 | 2 | 5 | 4 | 2,3 | 3,2 |
| El Capulín #1060 | 105 | 11.90 | 10.83 | 1.47 | 1.29 | 3 | 2 | 5 | 4 | 2,3 | 3,2 |
| El Capulín #1062 | 101 | 12.17 | 11.04 | 1.58 | 1.36 | 2 | 2 | 5 | 4 | 2,3 | 2,2 |
| El Capulín #1062A | 104 | 12.04 | 11.25 | 1.64 | 1.47 | 2 | 2 | 5 | 3 | 3,3 | 3,2 |
| El Capulín #1063 | 83 | 11.52 | 9.79 | 1.48 | 1.37 | 2 | 2 | 4 | 3 | 2,3 | 3,2 |
| El Capulín #1064 | 103 | 11.77 | 11.50 | 1.89 | 1.32 | 3 | 2 | 4 | 3 | 2,3,2 | 3,2 |
| Fort Kent | 61 | 10.57 | 9.01 | 1.36 | 1.31 | 3 | 3 | 3 | 2 | 2,2,2 | 3,2,2 |
| Hackberry | 52 | 10.55 | 9.90 | 1.59 | 0.92 | 3 | 2 | 3 | 1 | 1,2,2 | 1,1 |
| Harris Mammoth Yellow | 60 | 10.08 | 8.63 | 1.19 | 1.09 | 2 | 2 | 3 | 2 | 2,2 | 2,2 |
| Hickory King | 54 | 11.57 | 9.73 | 1.24 | 1.08 | 3 | 2 | 3 | 2 | 1,1 | 1,1,1 |
| India | 14 | 8.06 | 7.03 | 1.13 | 0.73 | 3 | 2 | 4 | 3 | 2,3,3 | 2,2 |
| Kerwo #1 | 90 | 11.94 | 10.30 | 1.17 | 1.36 | 2 | 3 | 4 | 3 | 1,2 | 1,2,1 |
| Kerwo #2 | 91 | 12.21 | 10.45 | 1.31 | 1.24 | 3 | 3 | 5 | 3 | 1,2,1 | 1,2,1 |
| Knighton Little Cob Flint | 56 | 13.09 | 10.97 | 1.35 | 1.07 | 4 | 2 | 4 | 2 | 1,1 | 1,1 |
| | | | | | | | | | | | 2,1 |
| Latham's Double | 55 | 12.23 | 11.28 | 1.63 | 1.26 | 3 | 1 | 4 | 1 | 1 | 1,2,2 |
| Longfellow #1 | 67 | 10.51 | 8.42 | 0.93 | 0.95 | 2 | 2 | 4 | 2 | 1,2 | 1,2 |
| Longfellow #2 | 69 | 11.51 | 10.72 | 1.52 | 1.33 | 3 | 2 | 4 | 3 | 2,2 | 2,3,2 |
| Louisiana Gourdseed | 57 | 12.18 | 11.56 | 1.54 | 1.23 | 4 | 3 | 3 | 1 | 1,1,1 | 1,1, |
| | | | | | | | | | | | 1,1 |
| Maíz chapolote | 47 | 9.32 | 8.53 | 1.26 | 1.05 | 4 | 3 | 4 | 2 | 1,2,2 | 1,1, |
| | | | | | | | | | | | 2,1 |
| Maíz de Elote | 80 | 10.98 | 9.82 | 1.33 | 1.26 | 3 | 2 | 4 | 3 | 1,2,2 | 2,1 |
| Maíz reventador (Coalcomán) | 45 | 9.02 | 8.26 | 0.95 | 1.01 | 2 | 2 | 3 | 1 | 1,1 | 1,1 |
| Maíz reventador (Kelly #3-4) | 51 | 11.80 | 10.97 | 1.53 | 1.01 | 4 | 3 | 4 | 3 | 1,2,1, 1 | 1,2,1 |
| Mandan Yellow Flour | 59 | 9.86 | 9.29 | 1.43 | 1.10 | 2 | 2 | 4 | 3 | 2,2 | 2,2 |
| Manglaralto | 34 | 8.85 | 7.50 | 1.00 | 0.85 | 2 | 1 | 2 | 1 | 1,2 | 1 |
| Papago (Lochiel Arizona) | 95 | 12.11 | 11.40 | 1.23 | 1.21 | 3 | 3 | 5 | 3 | 2,3,3 | 3,3,3 |
| Parker's Flint #1 | 64 | 10.27 | 9.44 | 1.22 | 0.96 | 3 | 2 | 4 | 3 | 2,2 | 2,2,2 |
| Parker's Flint #2 | 65 | 13.25 | 12.00 | 1.44 | 1.38 | 3 | 3 | 5 | 3 | 2,2,2 | 2,3,2 |
| Pia Oik #1 | 94 | 11.99 | 11.30 | 1.37 | 1.31 | 3 | 2 | 4 | 2 | 1,2,1 | 1,1 |
| Pia Oik #2 | 89 | 11.91 | 11.03 | 1.25 | 1.12 | 3 | 3 | 4 | 3 | 1,2,1 | 1,1,1 |
| Quito #8-4 | 35 | 8.80 | 7.81 | 0.95 | 0.95 | 2 | 2 | 4 | 3 | 2,3 | 3,2 |
| Quito #1-6 | 36 | 9.35 | 8.36 | 1.05 | 1.12 | 2 | 2 | 4 | 3 | 2,3 | 2,2 |
| Quito #9-3 | 37 | 10.23 | 9.10 | 1.11 | 1.09 | 2 | 2 | 4 | 3 | 3,2 | 2,3 |
| Quito #4-2 | 38 | 10.45 | 9.43 | 1.17 | 0.99 | 3 | 2 | 4 | 3 | 2,3,2 | 3,2 |
| Quito #6-1 | 39 | 11.98 | 10.79 | 1.29 | 1.10 | 3 | 2 | 4 | 3 | 2,3,1 | 3,2 |
| Río Loa | 22 | 9.87 | 9.68 | 1.28 | 0.87 | 2 | 1 | 4 | 2 | 2,2 | 2 |
| Sa 15 b-4 | 46 | 9.50 | 7.41 | 1.27 | 1.17 | 3 | 3 | 3 | 1 | 1,2,2 | 2,2,1 |
| San Andreas | 85 | 9.14 | 8.70 | 1.28 | 0.98 | 3 | 3 | 4 | 3 | 2,3,2 | 2,2,2 |
| | 78 | 11.42 | 10.63 | 1.75 | 1.20 | 3 | 2 | 4 | 2 | 1,1 | 1,2,1 |
| Santa Lucia #1 | 77 | 10.78 | 9.26 | 1.73 | 1.25 | 3 | 1 | 3 | 2 | 1 | 1,2,1 |
| Santa Lucia #2 | 74 | 8.27 | 6.08 | 1.21 | 1.05 | 2 | 2 | 2 | 2 | 1,1 | 1,1 |
| Santa Lucia #3 | 76 | 9.54 | 8.23 | 1.18 | 1.11 | 2 | 2 | 3 | 2 | 1,1 | 1,1 |
| Santa Lucia #4 | 79 | 10.82 | 8.66 | 1.42 | 1.21 | 3 | 2 | 3 | 2 | 2,1 | 1,2,1 |
| Santa Lucia #5 | 75 | 9.50 | 6.51 | 1.33 | 1.25 | 2 | 2 | 3 | 2 | 1,1 | 1,1 |
| Santa Lucia #6 | 50 | 10.07 | 9.90 | 1.32 | 1.27 | 4 | 2 | 5 | 2 | 1,1 | 1,1, |
| | | | | | | | | | | | 1,1 |
| Siamese Popcorn | 15 | 8.90 | 8.18 | 1.67 | 1.17 | 2 | 2 | 4 | 3 | 0,2 | 1,0 |

APPENDIX II (Continued)

| Name of variety | Figure number | Average length of glume (mm.) | Average length of median vein (mm.) | Average width of right margin (mm.) | Average width of right shoulder (mm.) | Average number of marginal veins | Average number of shoulder veins | Average size of keel vein* | Average size of median vein* | Average size of right Average size of right | Average size of right Average size of right shoulder veins* |
|--------------------|---------------|-------------------------------|-------------------------------------|-------------------------------------|---------------------------------------|----------------------------------|----------------------------------|----------------------------|------------------------------|--|---|
| Soledad #5075-1 | 26 | 10.32 | 8.75 | 1.34 | 1.39 | 2 | 2 | 3 | 2 | 2,1 | 1,1 |
| Soledad #5075-3 | 24 | 9.38 | 8.97 | 1.34 | 1.05 | 2 | 2 | 2 | 1 | 0,0 | 1,1 |
| Soledad #5075-5 | 25 | 10.52 | 9.88 | 1.58 | 1.11 | 3 | 2 | 1 | 1 | 1,1 | 1,2,2 |
| Soledad #5065-2 | 23 | 8.77 | 8.39 | 1.36 | 1.25 | 2 | 2 | 3 | 2 | 1,1 | 1,2 |
| Stevens Flint | 68 | 12.15 | 11.43 | 1.47 | 1.16 | 3 | 2 | 5 | 4 | 2,2 | 2,3,2 |
| Talpa | 48 | 9.56 | 8.64 | 1.36 | 0.80 | 4 | 1 | 3 | 3 | 2 | 2,2, 3,2, |
| Tama Flour Corn #1 | 70 | 12.73 | 11.75 | 1.16 | 1.08 | 3 | 3 | 4 | 3 | 2,2,2 | 2,3,1 |
| Tama Flour Corn #2 | 71 | 13.56 | 12.00 | 1.46 | 1.16 | 3 | 2 | 3 | 2 | 2,2 | 2,3,2 |
| Tennessee Red Cob | 58 | 13.39 | 13.14 | 1.68 | 1.25 | 3 | 2 | 5 | 1 | 1,1 | 1,2,2 |
| Titicaca #7700-5 | 31 | 9.46 | 8.40 | 1.38 | 1.31 | 2 | 1 | 4 | 2 | 2,2 | 2 |
| Titicaca #7729-2 | 32 | 10.08 | 7.90 | 1.81 | 1.35 | 2 | 1 | 5 | 3 | 2,2 | 2 |
| Titicaca #7729-5 | 33 | 10.38 | 9.14 | 1.69 | 1.27 | 3 | 1 | 4 | 2 | 2,3,2 | 2 |
| Toluca #1 | 82 | 11.77 | 10.69 | 1.45 | 0.97 | 3 | 2 | 4 | 3 | 2,2,1 | 2,2 |
| Toluca #2 | 81 | 9.14 | 8.07 | 1.07 | 0.99 | 2 | 2 | 3 | 2 | 1,2 | 1,1 |
| Topawa #1 | 88 | 12.10 | 10.83 | 1.41 | 1.02 | 4 | 2 | 4 | 2 | 1,1, 1,1 | 2,1 |
| Turkish Popcorn | 12 | 9.23 | 7.15 | 1.17 | 0.81 | 2 | 2 | 3 | 2 | 2,2 | 2,2 |
| Valle #6165 | 30 | 10.15 | 9.49 | 1.30 | 1.36 | 2 | 2 | 4 | 2 | 2,2 | 2,2 |

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